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### Studies on Costa Rican Odonata.

#### IV. *Erpetogomphus* in Costa Rica, with Descriptions of a New Species Having Complex Structural Mating Adaptations.

By PHILIP P. CALVERT, PH.D., University of Pennsylvania,  
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(Plate XVII)

The following summary of the geographical distribution of the genus *Erpetogomphus* was published in 1905 (Calvert, 1901-1908, p. 159): "A very characteristic genus of the present [Mexican-Central American] fauna. Eleven species are now known, ten of which have actually been found in Mexico or Central America. The eleventh, *E. compositus*, is known from Texas and Arizona, and will doubtless be found in Mexico; it has been reported from the Yellowstone and Oregon, which, with Ohio and Indiana (*E. designatus*), are the most northern known limits of *Erpetogomphus*. To the south, Guatemala is at present the known limit; there is, however, a very doubtful record from Brazil."

In 1907, in the supplementary part of the same volume (p. 398), it was possible to say: "The most southern locality for this genus certainly known is now San José, in Costa Rica, as

cited below under *E. elaps*"—a single male taken by the late Professor Biolley, in May, 1905, now in the British Museum of Natural History as part of the Godman-Salvin collection.

During the year which I spent in Costa Rica, I only once saw an insect which I thought might have been an *Erpetogomphus*. This was on the southern edge of Cartago, but I was unable to capture it, and repeated visits to the same spot on subsequent days failed to rediscover it. Its identity is therefore entirely uncertain.

In July, 1911, Professor J. Fidel Tristán, Senora Tristán and Senor C. Picado, went to Oricuajo, a farm belonging to Senor Santiago Guell, on the Pacific side of Costa Rica, between the Rivers Machuca and Jesus Maria, where they unit. Professor and Senor Tristán were here from July 5-10, and made a collection of Odonata which Professor Tristán subsequently sent to me. Among them was a male and a female *Erpetogomphus*, enclosed in the same envelope, so presumably taken pairing. This pair not only confirm the existence of the genus in Costa Rica, but are of an undescribed species which, in honor of my friend and companion on many a delightful excursion, I herewith describe as

*Erpetogomphus tristani*, n. sp. (Plate XVII).

♂ Vertex, clypeus, labrum, occiput and genae dark brown. Frons bright green, except for a superior transverse dark brown stripe in front of the antennae which is confluent in front of each eye with a narrower transverse dark brown stripe along the inferior margin. Labium, maxillae and bases of the mandibles pale yellow, but the apices of all brown or black. A nearly straight transverse ridge on the vertex behind the ocelli, forming a tubercle bearing some long dark hairs behind each lateral ocellus, but concealing only a small part of the occiput when the head is viewed from in front (Fig. 2). Hind margin of the occiput almost straight, curving slightly upward at each eye, with a row of moderately long dark hairs.

Fore and hind lobes of the prothorax pale green, the former tinged with pale brown on the sides. Middle lobe pale brown, a pair of sub-median dorsal dots and a larger spot each side pale green.

Thorax (meso-metathorax) with the mid-dorsal carina, borders of the ante-alar sinus, a mid-dorsal and a humeral stripe, and stripes on the first and second lateral sutures and along the ventral margin of the metepimeron, dark maroon brown. The median brown stripe is

narrowed at the antalar sinus (where it is narrowly confluent with the upper end of the humeral stripe of each side) and still more so at the transverse anterior mesepisternal carina, in front of which it widens anteriorly and is confluent on the mesinfraepisterna with the lower end of each humeral stripe. The pale antehumeral stripe is bright green, is wider at both ends than at its middle, where it is about two-thirds as wide as the brown median stripe and half as wide as the brown humeral stripe at the same level. The brown humeral stripe is constricted to half its width at its upper end where, as well as at its lower end, it is narrowly confluent with the brown stripe of the first lateral suture. This latter is twice confluent in its uppermost fourth with the brown stripe of the second lateral suture, which in its turn is confluent above (very narrowly) and below with the metepimeral brown stripe. The pale color of the sides of the thorax is more yellowish than the pale antehumeral stripe and is wider in each of its three divisions than the brown stripe which bounds each division posteriorly. Inter-alar dorsal sclerites pale green. Pectus pale obscure yellowish.

Abdomen brown, darker on segments 3-8, marked with pale yellowish-green as follows: most of 1; the auricles and two (?) posterior spots, one lateral (the other dorsal?), on 2; a narrow mid-dorsal stripe or line beginning at the anterior end of each of segments 3-7 but not reaching the hind end of any of them; a spot on each side in the foremost fourth on 3 or sixth on 4-6 (or 7?). Segments 9 and 10 are of a more reddish-brown than those preceding and bear a greater number of delicate pale hairs.

Abdomen widest at segment 1 and again at the articulation of 9 and 10. A tuft of pale hairs on a brown spot at the hind margin of 1 where dorsal and lateral surfaces meet. Auricles on 2 well-developed, decidedly projecting, with about eight minute denticles on the posterior margin. Segments 7-9 successively shorter, 10 longer than 8 or 9 but shorter than 7. Hind margin of 9 angularly produced into a mid-dorsal posteriorly-directed process. The hind dorsal margin of 10 is rounded and produced into a small rounded median tubercle which fits between the superior appendages.

Genitalia of 2 (Fig. 9) black; anterior hamules shorter than the posterior, rounded and hooked at tip, posterior hamules tapering to the acute straight tips. Each of the two antero-lateral angles of the vesicle of the penis terminating in a lamellate process.

Superior appendages three-fifths as long as 10, pale green, blackish at extreme base and at apex, with many hairs half as long as, or longer than, each appendage is thick. In dorsal view (Fig. 6) almost straight and parallel, the posterior half of each obliquely truncated from the outer side inward (mesad) and backward (caudad); at two-

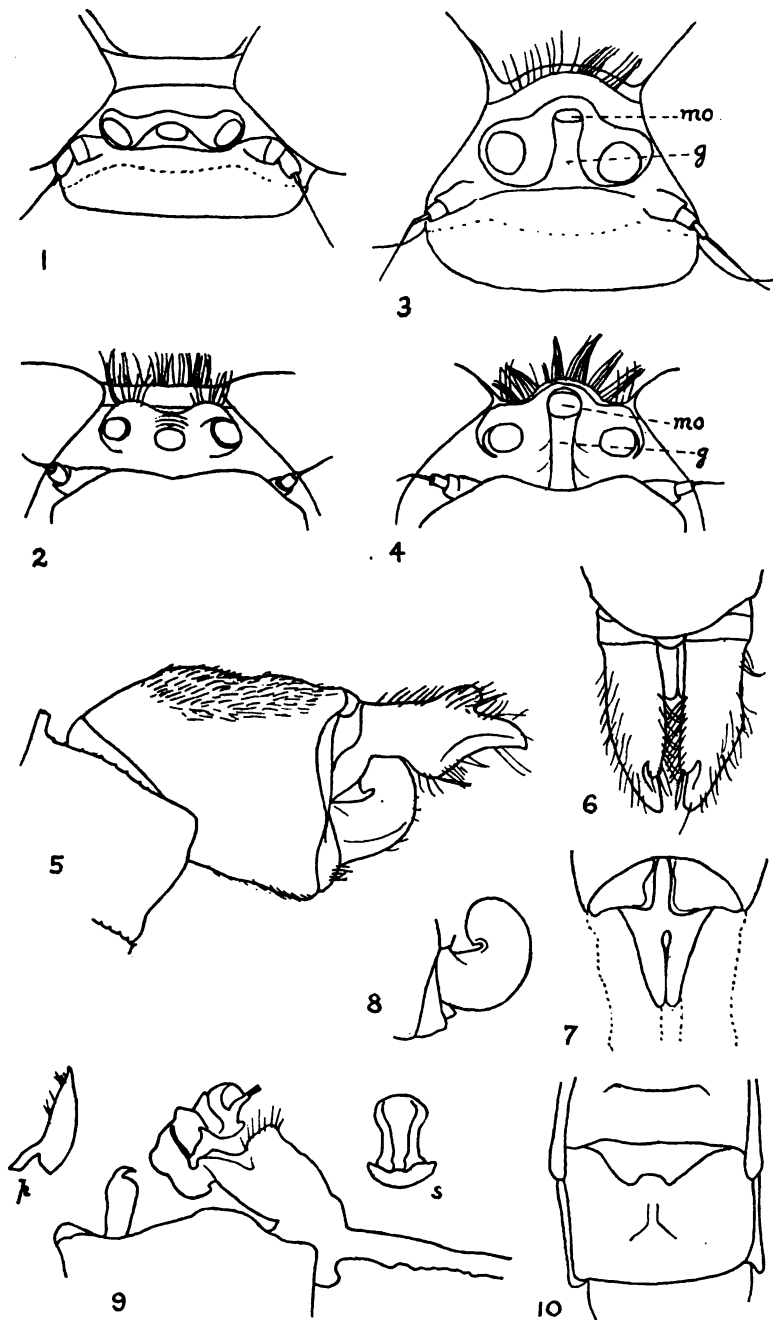
thirds length is a stout dorsal tooth on the inner (mesial) margin. In profile view (Fig. 5) each appendage at its base is almost half as high as the hind margin of 10 but contracts its height by one half on the ventral side of the proximal fifth; at one-half length is a strong tubercular ventral tooth directed ventrad, distad to this tooth the ventral edge is concave; the fourth sixth of the appendage's length on its dorsal edge is occupied by a stout tooth directed dorsad and caudad; from this tooth the thickness of the appendage gradually decreases to the apex which is obtuse and bent very slightly downward (ventrad). Viewed from below, each appendage has a ventral longitudinal carina in its proximal sixth and again in its distalf half.

Inferior appendage shining blackish brown, its hairs fewer and shorter than those of the superiors. Viewed in profile (Figs. 5, 8), it does not quite attain the level of the inferior tooth of the superiors; it is curved strongly dorsad, then cephalad and finally, at its apex, ventrad, decreasing gradually in thickness throughout its length. Viewed from below (Fig. 7), its width decreases from the base; it is divided into two branches from almost the base, the branches closely oppressed throughout and forming between them a deep ventral groove.

Femora dark brown, those of third legs redder, inner (lower) surface of first femora and a distal spot on inner surface of second pale green. Tibiae and tarsi black.

♀. Differs from the male as follows: Vertex with a deep median longitudinal groove on the posterior wall of which is situated the median ocellus; as a result, when the head is viewed from in front (Fig. 4), the median ocellus is above the level of the two lateral ocelli, and in dorsal view (Fig. 3) the median ocellus is completely posterior to the level of the other two. In the male, as in most Gomphinae, and indeed in Odonata generally, the median ocellus is below and at least not posterior to the level of the other two ocelli in these two views respectively (Figs. 2, 1). As a further result of the presence of this groove, the transverse ridge on the vertex behind the ocelli is produced in the middle dorsad and caudad as a marked convexity which conceals all of the occiput except its hind margin, when the head is viewed from in front. Dorsal surface of the occiput very much reduced antero-posteriorly, its hind margin strongly convex and fringed with dark hairs; posterior surface swollen in the middle, which is not the case in the male, and with a distinct socket on each side adjoining the compound eye. Front shallowly and widely grooved antero-posteriorly in the middle of its superior surface; this feature less marked in the male.

Mid-dorsal mesothoracic carina pale green; brown markings of the thorax paler, redder; green antehumeral stripe at mid-height half as wide as the brown mid-dorsal stripe.



ERPETO GOMPHUS TRISTANI—CALVERT.



Abdominal segment 2 with a mid-dorsal, and on each side a longitudinal, yellow stripe occupying the greater part of the length of the segment. Greatest width of the posterior half of the abdomen at the articulation of 8 and 9. Auricles on 2 very much smaller and not denticulated, as usual in this sex. Segments 7-10 successively shorter. Mid-dorsal posterior process of 9 shorter than in the male. Hind dorsal margin of 10 nearly straight, not produced. Eleventh segment a little shorter than the tenth, its tergite and sternites sub-equal. Terminal abdominal appendages as long as 10, pale brown, straight, conical, apices acute.

Vulvar lamina one-third as long as 9, its apical margin one-third as long as its base, shallowly concave (Fig. 10).

♂ ♀. Wings slightly smoky, tinged with faint yellow at the extreme base. Front wings with 14 (♂)-15 (♀) antenodals, 12-14 postnodals. Hind wings with 11 antenodals, 12-13 postnodals, anal triangle of ♂ 3-celled. Stigma dark brown.

*Dimensions.* Total length, ♂ 42, ♀ 44. Abdomen ♂ 31.5, ♀ 33.5. Hind wing, ♂ 28, ♀ 29. Costal edge of stigma, front wing ♂ 3, ♀ 3.5. Width of head ♂ 6, ♀ 6.3 mm.

*Hab.* Costa Rica, Oricuajo (Pacific side), July, 1911, by Prof. J. F. Tristán, 1 ♂, 1 ♀, now in the collection of the writer at the Academy of Natural Sciences of Philadelphia.

*Type.* The male above mentioned.

This pair show the following differences from the generic characters of *Erpetogomphus* as given in Biol. Centr.-Amer. Neur., pp. 146-147:

There are 9 (10 on the left side of the ♂) marginal cells on the front wings between M<sub>4</sub> and Cu<sub>1</sub> (short sector and first sector of the triangle) instead of 6-8 cells. I find in my notes, however, mention of a female *E. designatus* from Texas with 9-10 marginal cells.

There is but one row of cells in the anal and second cubital areas (postcostal area of de Selys) of the front wings from the base to beyond the level of the triangle; there are only two rows of cells at any point between Cu<sub>2</sub> (second sector of the triangle) and the hind margin in the male, but there are three rows for three (right) or four (left) cells in the female. These variations were met in the Biol. Cent. Amer. material also.

While the arculus is at or proximal to the second *subcostal* antenodal in seven out of the eight wings, it is not necessarily at or proximal to the level of the second *costal* antenodal, as the second subcostal antenodal is not coincident with the second costal antenodal in six out of the eight wings, but distal thereto. This lack of coincidence is often to be seen in this genus.



The sixth (instead of the fifth) antenodal is thicker on the left front wing of the female.

The abdomen of the male is widest at segment 9.

*Erpetogomphus tristani* ♂ falls under rubric AA of the key to the species of this genus (*Biol. Centr.-Amer. Neur.*, p. 160) so far as the superior appendages of the male are concerned, but the face has distinct dark markings. It is also allied to *E. ophibolus* of rubric A in possessing a superior tooth on the same appendages. In possessing both a superior and an inferior tooth, both well-developed, and such a strongly recurved inferior appendage, it differs from all other described species of *Erpetogomphus*.

The female *tristani* falls under rubric BBB of the same key (*l. c.*, p. 162) and in its occipital characters and brown antehumeral (+ humeral) stripe comes nearer to *diadophis* than to *designatus*, but differs from these and all other known species by the peculiar structure of the vertex, which deserves fuller mention.

Mr. Williamson (1899) first pointed out that in the Odonata Anisoptera, in pairing, the inferior appendage of the male rests on the top of the head of the female and the superior appendages of the male on the rear of the head of the female. He was able (1906) to make positive observations to this effect in the genus *Gomphus*, among others. Calvert (1906), in confirmation, figured the two sexes of *Aeshna constricta* [= *umbrosa*, E. M. Walker] in this position. There is no reason to think that the mating position in *Erpetogomphus* is different. In the above description and in the figures (Figs. 3, 4) of the vertex of the head of *E. tristani* female, mention is made of a deep median longitudinal groove (*g*), and of the great reduction of the dorsal surface of the occiput. On placing the head of the female and the hind end of the male abdomen side by side in the same field of the microscope, it is evident that the recurved terminal part of the inferior appendage of the male (Fig. 8) is sufficiently narrow transversely to be received into the median vertical groove of the female. It seems inevitable that the inferior appendage should fit into this groove when pairing takes place. It is also likely that the ventral tooth of each

superior appendage of the male is received into the socket on each side of the posterior surface of the female's occiput, and that the dorsal tooth of the same appendage is braced against her prothorax. *E. tristani* therefore furnishes one of the most complex structural mating adaptations hitherto noticed in the Anisoptera. In looking over the plates of de Selys & Hagen (1858) nothing so complicated is to be found in any species of this family figured therein.\*

#### LITERATURE QUOTED.

CALVERT, P. P. 1901-1908. *Biologia Centrali-Americana*. Insecta Odonata. London.

Id. 1906. Copulation of Odonata. *Ent. News*, XVII, pp. 148-150, pl. VII.

DE SELYS LONGCHAMPS, E. et. HAGEN, H. A. 1858. *Monographie des Gomphines*. Bruxelles, Leipzig, Paris.

WALKER, E. M. 1912. The North American Dragonflies of the Genus *Aeshna*. University of Toronto Studies. Biological Series, No. 11.

WILLIAMSON, E. B. 1899. A Note on Copulation among Odonata. *Ent. News*, X, pp. 42-43.

WILLIAMSON, E. B. 1906. Copulation of Odonata. *Ent. News*, XVII, pp. 143-148.

#### EXPLANATION OF PLATE XVII.

All the figures are of *Erpetogomphus tristani* n. sp. and have been drawn with the aid of the compound microscope and camera lucida. The magnification is the same in all, x 12.

Figs. 1 and 2. Dorsal and anterior views respectively of the vertex and occiput of the male. The dotted line in 1 shows the boundary between green and black on the superior surface of the frons.

Figs. 3 and 4. The same of the female. *g*, the vertical groove, *mv*, median ocellus.

Fig. 5. Left profile view of the apex of the male abdomen.

Fig. 6. Dorsal view of the superior abdominal appendages of the male.

Fig. 7. Ventral view of the inferior abdominal appendage of the male. Dotted lines show the proximal parts of the superior appendages.

Fig. 8. Left profile view of the inferior abdominal appendage of the male.

Fig. 9. Right profile view of the genitalia of the second and third abdominal segments of the male. *p*, posterior hamule and *s*, sheath of the penis, separated from the rest, *p* in lateral, *s* in posterior view.

Fig. 10. Ventral view of the 9th, and adjoining parts of the 8th and 10th, abdominal segments of the female.

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\*Since this paper was written, Dr. E. M. Walker's superb monograph of the North American *Aeshnas* has appeared (1912), in which he discusses (pp. 39-42) and figures (Plate 2) the copulatory position of *Aeshna*, *Gomphus* and other Odonata.



## THE CHILOPODA OF CALIFORNIA III

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### Suborder Geophiloidea

The members of this suborder are distributed over the entire earth but prefer the warmer and damper regions, the majority occurring in the northern hemisphere. They are to be found in damp places under stones, logs, leaves, the bark of trees and logs, and in the humus of woods and gardens into which they descend, especially during dry periods such as recur in California.

In all the body is elongate and very slender and consists of from thirty-one up to one hundred and eighty-one segments, as in a California species here described for the first time. The number of segments varies not only from genus to genus and species but, with few exceptions, also within the species, the range in some species being very great. The number in most cases is quite regularly longer in females than in males, though the maximum for the one ordinarily overlaps the minimum for the other. The antennæ are short and consist invariably of fourteen articles, excepting in occasionally met cases where the antennæ have been broken and are in process of regeneration. Eyes are always lacking. A basal plate, the tergite to which the prehensorial feet belong, is always well developed; while a small plate, remnant of a preceding tergite, may or may not show between it and the caudal margin of the cephalic plate. The cephalic plate may or may not possess a transverse suture, the frontal suture, setting off the frontal region. The mandibles may bear only so-called pectinate lamellæ, which consist of comb-like rows of slender bristles borne upon a common base or plate; or they may in addition, bear a strongly chitinated plate dentate along its distal edge, the dentate lamella, which, while usually entire, may be subdivided. The first maxillæ usually have their coxæ fused together at the median line to form a single plate or coxosternum, but, more rarely, they may be entirely separate; distad each maxilla presents an inner division and an outer one, the latter, the palpus, being usually biarticulate but sometimes entire; at the distal exterior angle of each coxa and of the first joint of the palpus proper there may be a membranous process or lappet. The second maxillæ, often spoken of together as the labium, usually have the coxæ fused in the middle line, though, as with the first pair, they may remain distinct; the palpi are, in all known California species, triarticulate and may or may not terminate in a claw. Each leg-bearing segment excepting the first and the last bears a pair of spiracles, each spiracle opening through a sclerite in the pleural region. The coxopleuræ (pseudopleuræ, pleuræ) of the last segment give exit through the so-called coxopleural pores to a number of glands which may be many or few and may open separately or into one of two common larger pits at the edge of the last ventral plate.

The fauna of California includes an exceedingly interesting representation of this suborder, showing a greater variety and richness than in any other section of the United States. The Californian families known may be thus separated.

## Key to Families of the Suborder Geophiloidea

- a. Mandible with a dentate lamella and with one or more pectinate lamellæ.
  - b. Antennæ flattened, broad at base and attenuated distad; mandible with several pectinate lamellæ. Family *Himantariidae*
  - bb. Antennæ cylindrical, filiform, not broad at base and attenuated distad; mandible with a single pectinate lamella. Family *Schendylidae*
- aa. Mandible without any dentate lamella; with one or several pectinate lamellæ.
  - b. Mandible with two or more pectinate lamellæ; coxæ of first maxillæ entirely separate from each other; pleuræ of prehensorial segment exposed each side of basal plate.
    - c. Coxæ of second maxillæ broadly coalesced at middle; mandible with several pectinate lamellæ. Family *Mecistocephalidae*
    - cc. Coxæ of second maxillæ entirely separate; mandible with but two pectinate lamellæ. Family *Arrupidae* fam. nov.
  - bb. Mandible with but a single pectinate lamella; coxæ of first maxillæ fused with each other at least proximally; pleuræ of prehensorial segment not exposed each side of basal plate.
    - c. Labrum entire, uniformly chitinized, coalesced with the cephalic plate excepting at ends; hypopharynx strongly developed; palpi of first maxillæ thick, strongly arched together in a semicircle. Family *Tampiyidae* fam. nov.
    - cc. Labrum free (in ours); tripartite, or with the divisions clearly traceable if secondarily coalesced; hypopharynx not unusually developed; first maxillæ not thus strongly arched in a semicircle.
      - d. Median piece of labrum extending along surface of the lateral with which it is fused at least in part; at middle the edge bears two conspicuously larger and more strongly chitinized teeth; chitinous lines of prosternum well developed. Family *Soniphilidae*
      - dd. Median piece of labrum entirely free, not bearing at middle two teeth conspicuously larger and more strongly chitinized than those adjacent; chitinous lines absent or but weakly developed. Family *Geophilidae*

Family *Mecistocephalidae*

In this family the cephalic lamina is long and relatively narrow. The antennæ are filiform. The prehensorial feet are strongly developed and much exposed at sides of head from above, the pleuræ of the segment also being distinctly exposed at the sides of the basal plate which is narrow. A prebasal plate is never present. The labium is tripartite with the median piece very narrow, its sides being parallel or nearly so. The mandibles bear several pectinate lamellæ but no truly dentate plate. The coxæ of the first maxillæ remain entirely distinct. No suprascutella or plates between tergites and spiraculiferous sclerites present. The coxopleuræ are pierced with numerous pores which are mostly

scattered over the entire surface. Anal legs with six articles distad of the coxopleuræ.

*Mecistocephalus* is the only North American genus of the family at present known.

### Genus *Mecistocephalus* Newport

In this genus the head is very large with the cephalic lamina much longer than wide and uniformly narrowed from the front caudad. The antennæ are rather large and are a little attenuated from the proximal and distad. The labrum has the middle piece very narrow and acutely pointed distad while the side pieces bear a fringe of very short pectinæ. In the first maxillæ the branches are membranous distad. Anal legs without claws.

So far as known the number of legs is invariable for each species.

In California there are two species of this genus, *M. limatus* Wood and *M. anomalus* Chamberlin, which are easily separated on the basis of the number of pairs of legs, the former having forty-five and the latter forty-one pairs.

### *Mecistocephalus limatus* Wood

This is one of the commonest members of the Geophiloidea in the central portion of the state and also ranges to the southern portion, though it is not often met with during the dry season. During the rainy months it often occurs in great numbers under the fallen leaves of wooded areas. It seems to be especially abundant about San Francisco Bay.

A large robust species often attaining a length of 60 mm. or more, while the head as a whole may be 2.5 to nearly 3 mm. across in large individuals. The body is conspicuously attenuated from the head caudad. The head and body are polished shining. Head and antennæ dark reddish or chestnut in color; body and legs orange or rusty yellow, the dorsal scuta, especially on anterior portion of body, often with a narrow dark band along caudal edges. Antennæ long, attenuated distad. The claws of the prehensors when closed extend nearly to the distal end of the first antennal article, each prehensor armed with four strongly chitinized teeth, one on each article, of which those of the first article and claw are largest. Anterior sterna with a deep longitudinal median sulcus which becomes less strongly developed caudad. First spiracle much larger than the second, vertically elliptical, the others circular or nearly so. Last ventral plate strongly narrowed caudad, triangular. Coxopleuræ of last segment with numerous small pores and usually one larger one distributed over most of the surface, the number few in immature individuals. Pairs of legs in both sexes, so far as observed invariably forty-five.

Specimens have been examined from the following localities: Mill Valley, Sausalito, Berkeley (author); Stanford (Mann); and Claremont (Pomona College collection).

### *Mecistocephalus anomalus* Chamberlin

This species in size, coloration and general structure is very close to the preceding one. It is readily separated in having invariably forty-one pairs of

legs as against the forty-five in *limatus*. The antennæ are typically smaller and shorter.

Found by the author to be very common during the wet season about Monterey Bay. Also taken at Oroville (April, 1911). In both of these places it appears wholly to replace *limatus*.

Family **Arrupidæ** fam. nov.

Differs from the preceding family (as represented in California) in having the three divisions of the labrum, of which the median is larger, entirely unarmed; in having the coxæ of the second maxillæ entirely separate; and in having the mandible with but two pectinate lamellæ.

Verhoeff's superfamily name *Placodesmata*, proposed for the *Mecistocephalidae*, may now, with better service, be employed to indicate the group formed by this family and the *Arrupidae*.

Genus **Arrup** gen. nov.

Labrum strongly chitinized, edges all smooth; the median piece broadly triangular, with the apex directed caudad. First maxillæ with the outer branch long, entire, membranous distad; no lappets. Palpus of second maxillæ triarticulate, without a claw. Last ventral plate wide, triangular; coxopleural pores few, small. Antennæ thick, sub-filiform. First joint of prehensors with a large, conical, strongly chitinized tooth; other joints unarmed. Anal legs unarmed.

Type.—*Arrup pylorus* sp. nov.

**Arrup pylorus** sp. nov.

Attenuated cephalad, more strongly caudad. Dorsum with a sharply impressed longitudinal median sulcus. Fulvous in color; head light reddish brown. Head widest anteriorly, narrowed to caudal margin which is truncate; anterior margin extended forward from sides to middle. Antennæ short, thick; all articles short, decreasing from basal ones to the penult; ultimate longer than the two preceding taken together. Basal plate overlapped by the cephalic; exposed portion very short, but little more than one-seventh as long as the cephalic, 4.8 times wider than long. Spiracles all circular, the first very much larger than the second. Last ventral plate wide, triangular, the sides converging caudad to meet at an angle. Coxopleural pores three or four on each side, small, adjacent to edge of last ventral plate. Anal legs in male crassate. Pairs of legs, forty-one. Length, 22 mm. (type).

Localities.—Sausalito and Berkeley (author, April, 1911).

Family **Tampiyidæ** fam. nov.

Labrum of one, uniformly chitinized piece, which is firmly coalesced with the labrum excepting at the ends where the suture may be detected; median portion conspicuously protuding, armed caudad with few stout teeth, the lateral portions pectinate. First maxillæ with outer branch distinctly biarticulate, the first article with a lappet, the apical joint thick, strongly bent inward and contiguous with its fellow. Palpi of second maxillæ triarticulate, ending in claws, which are simple, not toothed or pectinate. Prosternum with strongly developed

chitinous lines; its anterior median margin armed with two stout conical teeth. Suprascutella absent. Ventral pores absent. Antennæ flattened but of equal width from base to apex, being not at all attenuated. Pores of coxopleuræ scattered.

This family is evidently very close to the *Gonibregmatidae*, a family occurring in the Philippines and East Indies, with which it forms a natural group. One genus at present known.

#### Genus *Tampiya* gen. nov.

Lateral portions of the labrum concave, each pectinate with few lightly chitinized processes or spines, the middle portion protruding caudad and distally truncate, bearing a row of stout, conical, highly chitinized teeth. Lappets of first maxillæ very long. The claw of palpus of second maxillæ long, smooth. Cephalic plate not wholly covering the prehensorial feet. Basal plate short, wider than cephalic plate. Chitinous lines very strongly developed. Anal legs with large claws. Hypopharynx strongly developed, bifurcate anteriorly. Spiracles all circular. Last ventral plate moderate; pores scattered over coxopleuræ.

Type.—*Tampiya pylorus* sp. nov., the only species thus far known.

#### *Tampiya pylorus* sp. nov.

Cephalic plate truncate caudad, the sides conspicuously convex, anterior portion sub-triangular; about equal in length and breadth. Antennæ rather narrow, flattened, of uniform width throughout. Palpi of second maxillæ conspicuously flattened. Basal plate very wide, wider than head, about three and a half times, or a little more, wider than long. Prehensors when closed with claws almost even with front margin of head; joints all unarmed. Anterior median margin of prosternum armed with two stout conical teeth. Spiracles all circular, the first not specially enlarged, those of ultimate segments becoming very small. Last ventral plate rather narrow, short, caudal margin a little incurved. Coxopleural pores large, eight or more on each side, mostly scattered over coxopleura, free from plate but a few covered by edge of the latter. Anal legs short, ending in stout claws. Pairs of legs, one hundred and twenty-five.

Locality.—Sausalito.

#### Family Geophilidæ

In this family the labrum is tripartite, the middle piece varying in relative size. The mandible bears but a single pectinate lamella and no dentate lamella. The coxæ of the first maxillæ are coalesced at the middle. No suprascutella are present. The subfamilies represented in California may be distinguished by means of the following key:

#### Key to Subfamilies

- a. The coxosternum of second maxillæ with halves nearly separated at middle; on each side a strongly chitinized suture running from the ecto-caudal angle cephalo-mesad (pleuro-sternal suture). ▢ Subfamily *Chilenophilina*.



aa. Coxosternum with halves well united at middle; no such pleuro-sternal suture present.

b. First maxillæ without lappets; middle piece of labrum very large, overlapping the ends of the short lateral pieces, which are unarmed, dentate along its anterior edge; dorsum not bisulcate.

Subfamily *Linoteniinae*

bb. First maxillæ with well developed lappets; middle piece of labrum small, the dentate margin caudad, lateral pieces pectinate, dorsum bicusate.

Subfamily *Geophilinae*

#### Subfamily *Geophilinae*

The two California genera belonging to this subfamily may be separated thus:

#### Key to Genera

a. Joints of prehensorial feet not dentate within; anal legs ending in claws.

Genus *Geophilus* Leach

aa. Joints of prehensorial feet dentate within; anal legs not terminating in claws, the claw being replaced by a small seventh article.

Genus *Arenophilus* Chamberlin

#### Genus *Geophilus* Leach

In this genus the prehensorial feet, for the most part, do not extend beyond the front margin of the head and are unarmed within or with but rudiments of denticles at base of claw. The basal plate is wide. In most species the last ventral plate is wide but in some it is but moderate or even narrow. The anal legs end in claws. The middle piece of the labrum is usually dentate and the lateral ones pectinate. In the species here included as belonging to the Californian fauna the ventral pores are numerous and arranged in a transverse band immediately in front of the caudal margins of sternites.

The three known Californian species may be separated by means of the following key.

#### Key to Species

a. Prebasal plate exposed; last ventral plate very wide; coxopleural pores in adults covered by edge of ventral plate.

b. All spiracles circular; claws of prehensorial feet extending beyond front margin of head. *G. rubens* Say.

bb. Anterior spiracles elliptical; claws of prehensorial feet not extending beyond front margin of head. *G. regnans* Chamberlin

aa. Prebasal plate not exposed; last ventral plate narrow; coxopleural pores small, a dozen or more on free surface of coxopleura.

*G. nasintus* Chamberlin

#### *Geophilus rubens* Say.

Robust; attenuated caudad but not cephalad. Typically there is a geminate and often interrupted black band along the dorsum, though this may be entirely

absent; the body otherwise testaceous, the head with prehensorial feet darker as usual. The spiracles are all circular. In the eastern states, where this species is common, the pairs of legs number most frequently forty-nine to fifty-one in the male and fifty-one to fifty-three in the female; but in Californian specimens studied, the numbers are most frequently fifty-nine to sixty-one, though in one specimen but forty-seven were present.

Two of the Californian specimens studied were collected on a sandy beach at Pacific Grove by Miss Helen Nagel of Stanford, to whom I am indebted for the same. They are large specimens which are paler than usual and lack the dorsal dark band. The author has collected it also at Oroville (April, 1911). A specimen collected at Claremont is among material received from Prof. Baker. Wood reported three specimens, presumably this same species, from the Santa Cruz Mountains under the name *G. laevis*.

#### ***Geophilus regnans* Chamberlin**

A large species in which the body is wide anteriorly and attenuated caudad much as in the preceding species. The anterior spiracles are obliquely elliptical, the median and caudal ones circular. The number of pairs of legs is mostly from seventy-seven to eighty-five, seventy-nine and eighty-one being perhaps commonest. The length may be up to 70 mm.

Evidently an abundant species in southern California. Numerous specimens have been seen from the following localities: Claremont (Baker), Los Angeles and Pacific Grove (author). It seems to be the commonest *Geophilio* about Claremont.

#### ***Geophilus nasintus* Chamberlin**

Of nearly same form as the preceding, being narrowed but little cephalad and strongly caudad. Fulvous in color, the head and prehensorial feet darker, reddish. No frontal suture evident. The claws of the prehensorial feet when closed about even with the front margin of the head. Spiracles all circular. The pairs of legs in the type specimen number seventy-three and the length of body is 42 mm.

The exact locality from which the type came is uncertain; but the vial was among material from southern California received from Prof. Baker and is assumed to be from that region.

#### **Genus *Arenophilus* Chamberlin**

In the species belonging to this genus at present known a frontal suture is evident and the prebasal plate is absent or covered. The basal plate is trapeziform and conspicuously narrowed cephalad. The tripartite labrum has the free margin of all the divisions pectinate, the processes of the lateral ones being long and close set. The prehensorial feet are large and much exposed from above and the claws when closed extend well beyond the front margin of the head; the articles dentate within. The ventral pores are numerous and arranged in a single condensed area on each sternite upon which occurring. The last ventral plate is very wide. Each coxopleura with one or two large pits at or beneath edge of

ventral plate. Anal legs clawless, the claw in each being replaced by a small additional article.

One species occurs, somewhat doubtfully, within the state.

### *Arenophilus bipunticeps* Wood

Cephalic plate truncate caudad and extending over the anterior border of basal plate; bearing two sharply impressed sulci on caudal portion which diverge but little cephalad. Claws of prehensorial feet when closed extending much beyond anterior margin of head, the teeth of joints usually small. First spiracle vertically elliptic, larger than the second; the immediately following spiracles may also be similar in shape, those of more caudal segments becoming gradually circular. Ventral pores in a large area in front of caudal margin which is truncate cephalad and extended angularly at middle caudad. Coxopleuræ typically with two large porigerous pits at each lateral edge of ventral plate; in some specimens the more caudal pit on each side may be broken into two distinct but contiguous pits.

A large species which has a large head from which the body is narrowed caudad.

Two specimens in a vial containing no locality label but among others from Claremont and undoubtedly collected at that place. In the eastern section of the United States this is one of the commonest and most widespread members of the suborder.

### Subfamily Linoteniinæ

Of the two American genera at present known as belonging to this subfamily, one, *Linotenia*, occurs in California.

The labrum has the middle piece relatively very large and toothed along the margin directed cephalad whereas the side pieces are small, in part overlapped by the median, and with edges wholly smooth or free from teeth or pectinæ. The palpi of the first maxillæ lack lappets. The dorsal plates are smooth, not bisulcate as in the preceding subfamily. Ventral pores in a well marked transverse band in front of caudal margin, the band on more caudal segments usually divided at median line.

### Genus *Linotenia* C. Koch

This is a compact and clearly delimited genus. The species all have the body decidedly narrowed cephalad with the head small and characteristically narrowed anteriorly. The frontal suture is distinct. Antennæ filiform. The claws of the prehensorial feet, which when closed, do not extend beyond the front margin of head and usually fall considerably short of it, bear at base within each a conspicuously large tooth. The coxosternum, or prosternum, is without lateral chitinous lines. The coxopleuræ bear several to many small pores. The anal legs terminate in claws.

Most species of the genus in life are bright reddish in whole or in part; but in alcohol the red pigment fades leaving the color mostly some shade of brown.

But one species is known at present as occurring in California, this being the large and widespread *L. laevipes* Wood.

***Linotenia laevipes* Wood**

Syn. *Strigamia parviceps* Wood

*Strigamia epileptica* Wood

*Scolioplanes imperialis* Brolemann

*Linotenia rubelliana* Chamberlin

This handsome species occurs throughout most of California and ranges northward into Washington. It may attain a length of 90 mm. or more. In life the entire animal is red, but quickly fades in alcohol, the head with prehensorial feet and antennæ usually retaining a deeper color. The body is robust and conspicuously attenuated at the ends as usual. While usually free, the caudal angle of the head may be covered by the basal plate, this being more frequently the case apparently in the males than in the females. The tooth at base of claws

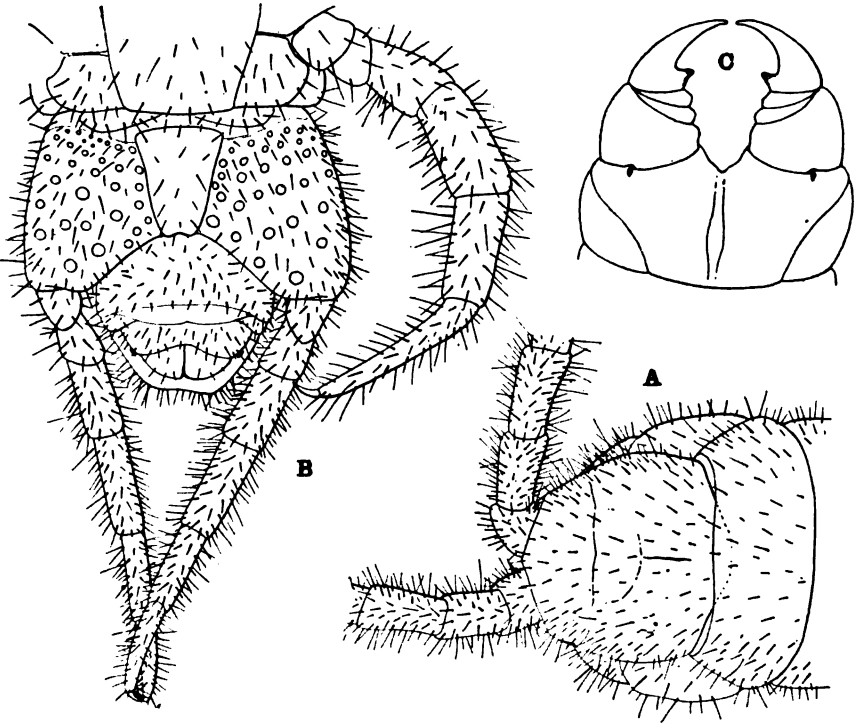


**Figure 217**

A, Dorsal view of anterior region of a female specimen of *Linotenia fulva* (Sager) from Saluda, N. C., showing cephalic plate crossed by frontal suture, the broad basal plate overlapping the caudal angle of the cephalic, the prehensorial feet partly exposed at sides of head, and the proximal portion of antennae. B, Ventral view of the posterior end of the same specimen, showing the enlarged coxopleuræ pierced by the numerous coxopleural pores, the narrow last ventral plate or sternite between them, etc. C, The prosternum and prehensorial feet of the Californian *Linotenia laevipes* (Wood), showing the characteristically large tooth at the base of each claw within.

of prehensorial feet very large (see figure). Spiracles all circular, the first not visibly larger than the second. Last ventral plate very wide, strongly narrowed caudad. Coxopleuræ with numerous small pores and usually on two larger ones, all arranged along and beneath the edges of the ventral plate. In immature specimens often only the two larger pores on each side evident. Anal legs in female slender, about equalling the penult in length, ending in a long claw; in the male greatly enlarged and flattened dorso-ventrally. In the Californian specimens examined the number of pairs of legs varies mostly from sixty-nine to seventy-five but often falls to sixty-seven and may be as large as ninety-one, as in a specimen from Oroville.

I have seen specimens from the following localities: Oroville, Pacific Grove, Berkeley, Stanford and Santa Barbara (author's collection), and from Claremont (Prof. Baker).

Subfamily *Chilenophilinæ*  
(*Ribautiina* of Brolemann)

This recently established subfamily is proving to be a large one, a considerable number of genera now having been found to belong to it. The group is readily distinguished by characters of the second maxillæ, these having the two halves of the coxosternum almost separated at the middle and each presenting a very conspicuous, strongly chitinized suture extending from the caudo-external angle meso-cephalad. Three genera are represented in California.

Key to Genera

- a. Side pieces of labrum extending over the middle one and meeting at the median line; and legs ending in a strongly developed claw.

Genus *Gnathomerium* Ribaut

- aa. Side pieces of labrum completely separated by the middle one; anal legs clawless or ending in a rather weakly developed claw.

- b. Femur of palpus of second maxillæ with a distinct process at distal meso-dorsal angle; anal legs ending in a small membranous seventh article which replaces the claw. Genus *Watophilus* Chamberlin

- bb. Femur of palpus of second maxillæ with no such process; anal legs with but six joints and clawless or with a weak claw.

Genus *Taiyuna* gen. nov.

Genus *Gnathomerium* Ribaut

This genus is represented in North America by several species of which one is known to occur in California. A second species, *G. utahensis* Chamberlin, common in Utah, may range into the mountains of this state.

The species of this genus are typically widest anteriorly and attenuated from the head caudad. The lateral pieces of the labrum extend mesad over the middle piece and are contiguous with each other at the middle line, the edge of the middle piece bearing teeth which project out from beneath, the lateral pieces fringed with pectinæ. Palpus of second maxilla triarticulate, all articles lacking special processes. Ventral pores not in definite areas. The anal legs consist of the usual six articles, the ultimate ending in a well developed claw.

**Gnathomerium melanonotum** WoodSyn. *Mecistocephalus limatus* Wood*Mecistocephalus quadratus* Wood*Geophilus glaber* Bollman

This is a widespread species on the Pacific Coast, ranging throughout most of California and northward to Canada. It is conspicuously attenuated from the head caudad, resembling in its proportions a *Mecistocephalus*. The head and antennæ are reddish brown, the latter tipped with pale; the body is of the usual brownish yellow color but having in most a decided greenish or olivaceous tinge; along the dorsum there is commonly a black stripe which is mostly geminate or double. The cephalic plate is attenuated caudad, widely rounded posteriorly. Frontal suture distinct. Prebasal plate not exposed. The claws of the prehensorial feet when closed extend beyond the front margin of the head much; first joint and claw armed within with well developed teeth, the intermediate articles with inconspicuous denticles. The first spiracle nearly circular, being slightly vertically elliptic, and it is much larger than the second. The last ventral plate is moderately wide. The coxopleuræ bear a number of mostly small pores both below and above. The number of pairs of legs varies mostly from forty-seven to fifty-five, forty-nine and fifty-one being common, and in the southern part of the state the number ranges prevailingly from fifty-nine to sixty-five pairs. Adults mostly from 35 to 50 mm. in length.

Specimens from within the state have been seen from the following localities: Shasta Springs, Oroville, Pacific Grove, Point Lobos, Sausalito, Berkeley and Stanford (collected by writer), and from Claremont and neighboring mountains (Prof. Baker, collector).

**Genus Taiyuna** gen. nov.

Head large, the body scarcely narrowed cephalad, strongly so caudad. The labrum with side pieces lapping well over the ends of the middle one but not contiguous mesally; middle pieces with many closely set, stout spines on free edge, the lateral pieces with comparatively few, these being bent strongly mesad. Palpi of first maxillæ with long membranous lappets. Palpi of second maxillæ wholly without processes. Ventral pores not detected. Last ventral plate narrow. Coxopleuræ with a number of small pores. Anal legs composed of six articles beyond Coxopleura; claw absent or rather slender if present.

Type.—*Taiyuna occidentalis* Meinert.

**Taiyuna occidentalis** MeinertSyn. *Geophilus californiensis* Bollman.

This species is widespread in the state and shows corresponding variation. The number of pairs of legs in specimens about San Francisco, the type locality, varies from sixty-seven to seventy-five, seventy-one and seventy-three being commonest; but, as usual with members of the group, in going south the number increases. At Los Angeles the author found individuals with as high as eighty-seven pairs (*isantus* Chamb., var.) which seemed distinct until more abundant

material indicated intergradation. Mr. Bollman's *californiensis* seems to have been based on partly grown specimens of this species, his description agreeing completely with such so far as it goes.

Body as wide or nearly as wide anteriorly as at the middle, but strongly narrowed caudad. Head and prehensorial feet with prosternum brownish red; antennæ brown, pale distad; body fulvous, more brownish cephalad; legs yellow. Cephalic lamina longer than wide, narrowed from in front caudad. Prebasal plate not evident, the cephalic overlapping the anterior border of the basal. Claws of prehensorial feet when closed reaching well beyond the first antennal article; first joint of prehensor with a tooth at meso-distal angle, the claw at base also with a somewhat smaller tooth. In large specimens the first spiracle is distinctly vertically elliptic and much larger than the second, all others circular. The last ventral plate moderate in width, longer than wide, narrowed caudad. Coxopleuræ with from four or five to thirty-nine or so, the larger numbers occurring in individuals not fully grown; some of the pores usually covered by edges of ventral plate, while one, often larger, usually stands apart from the rest on the more caudal surface of the coxopleura. Pairs of legs sixty-seven to eighty-seven. Length up to nearly 70 mm.

Localities.—San Francisco, Sausalito, Berkeley, Stanford, Pacific Grove, Monterey, Santa Barbara and Los Angeles, collected by the writer. A single specimen is also in the material received from Pomona College (Pillsbury, collector).

### **Taiyuna claremontus** Chamberlin

This species is known from but few specimens, mostly from Claremont. It differs from the preceding in having the anal legs armed with a distinct claw. The number of pairs of legs in the type is sixty-five and the length 49 mm.

### **Genus Watophilus** Chamberlin

Labrum with middle piece fully separating the lateral. First article of palpus and coxa at disto-ectal angles bearing long lappets. Coxæ of second maxillæ nearly separated mesally; the palpus with femur at meso-dorsal distal angle with a conical process and usually the succeeding article less distinctly produced at disto-ectal angle. Prosternum without chitinous lines. Claws of prehensorial feet extending beyond front margin of head; articles of feet dentate within. Ventral pores absent. Last ventral plate wide. Coxopleural pores small, few. Anal pores present. Anal legs clawless, the claw being replaced by a small, membranous, seventh article. There is a tendency for the number of pairs of legs to be fixed for each sex in each species, variations from this mode not being frequent. The two California species known may thus be separated.

### **Key to Species**

- a. Pairs of legs forty-one to forty-three; exposed portion of basal plate eight times wider than long. *W. errans* sp. nov.
- aa. Pairs of legs forty-seven to fifty-five; exposed portion of basal plate about three and one-half times wider than long. *W. laetus* sp. nov.

*Watophilus errans* sp. nov.

A small species under 13 mm. in length and seeming to have constantly forty-three pairs of legs in the female and forty-one in the male. The body is yellowish white with the head of a pale reddish cast. The cephalic plate is elongate with the sides weakly convex, a little converging at ends, more so cephalad; caudal border truncate, overlapping considerably the basal plate, the exposed portion of which is very short, being eight times wider than long, and is marked with a distinct longitudinal median sulcus. No frontal suture is present. The antennæ are short and strictly filiform. The claws of the prehensorial feet when closed extend beyond front margin of head; claw armed at base with a stout conical tooth, the first joint armed near distal end with a somewhat larger conical tooth. First spiracle subelliptic, larger than the second, others circular. Last ventral plate wide. Coxopleural pores small, few, mostly covered.

Locality.—Berkeley, Cal., (author, April, 1911).

*Watophilus lætus* sp. nov.

Head with sides nearly parallel, a little converging caudad, but slightly excurved; caudal margin truncate. The anterior nearly so; corners not strongly rounded; much longer than wide (5:4). Basal plate much covered by cephalic, the exposed portion about three and one-half times wider than long, one-quarter as long as head. Antennæ longer than in the preceding species. Claws of prehensorial feet when closed extending a little beyond front margin of head; tooth of claw small. Prosternum wider than long (11:9). Last ventral plate wide, sides converging caudad, caudal margin a little incurved. Coxopleura pores few, partly covered. Distal joint of anal legs long and slender. Anal legs in male crassate proximally, the four distal articles slender. Pairs of legs, forty-seven to fifty-five. Length about 15 mm.

Localities.—Stanford (Mann), Pacific Grove and Berkeley (author). The type is from Berkeley.

## Family Soniphilidæ

Of the three genera at present known to belong to this family, two occur in California. They are characterized by having a coalescence between the parts of the labrum, the middle piece widely extending along the lateral to their outer ends in most cases where, at least fusion is evident; at the middle of the free edge two decidedly larger and more strongly chitinized teeth are borne, the adjacent ones being abruptly smaller, these middle teeth with in some several adjoining pairs in two of the genera extending directly; ventrad rather than caudad; lateral portions of edge pectinate. The first maxillæ may or may not bear well developed lappets. Second maxillæ without pleuro-sternal suture, the coxæ broadly joined at middle. Chitinous lines of prosternum strongly developed. Anterior border of each anterior sternite is furrowed transversely, the furrow being guarded ventrally as a rule by a chitinous rim or flange beneath which fits the edge of the preceding plate.

The three genera may be separated by means of the following key:



## Key to Genera

- a. Joints of prehensorial feet not dentate within; claws not extending beyond the front margin of head; last ventral plate very wide.
- b. Edge of labrum bent centrad at middle, its teeth extending in same direction; coxa of first maxilla without lappet, the proximal article of palpus with a conical process or lappet which is shorter than the distal article.  
Genus *Soniphilus* Chamberlin
- bb. Edge of labrum at middle with teeth directed caudad; first maxilla with coxa and proximal joint of palpus with long lappets.  
Genus *Tabiphilus* gen. nov.
- aa. Some joints of prehensorial feet dentate within; claws when closed extending beyond front margin of head; last ventral plate but moderate in width.  
Genus *Poaphilus* Chamberlin

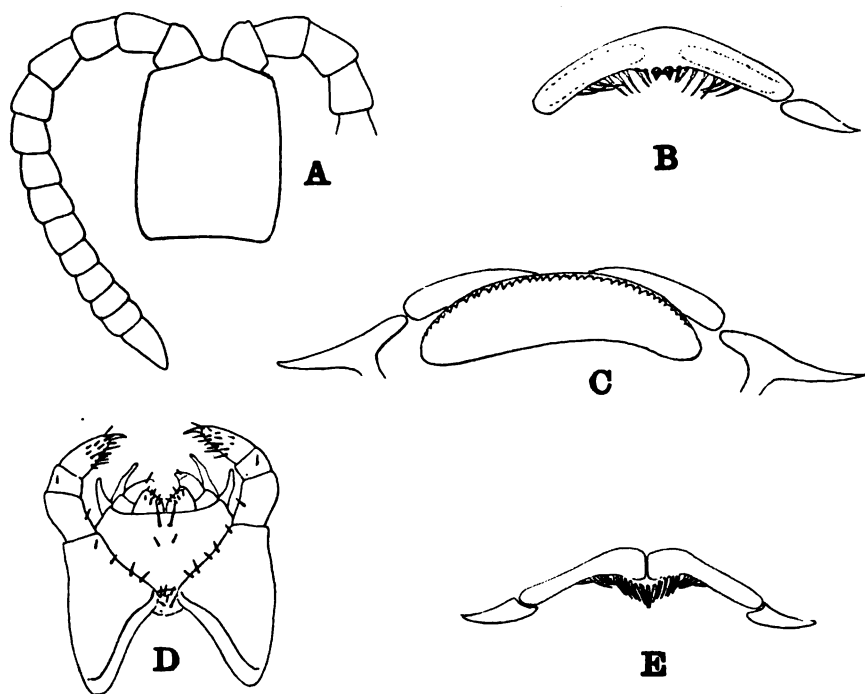


Figure 218

A, Dorsal view of cephalic plate and antennæ of *Soniphilus secundus* sp. nov. B, Cephalo-ventral view of labrum of the same, showing the two large middle teeth and the outlines of the lateral pieces over which the median extends. C, Labrum of *Linotenia laevipes* (Wood), showing the large median piece which is dentate along the edge directed anteriorly, and the smooth lateral pieces with the lateral supports or laminae fulcraentes. D, First and second maxillæ of *Gnathomerium melanonotum* (Wood), showing the divisions of the first with the membranous lappets on each side, and, in the second, the conspicuous pleura-sternal sutures. E, Labrum of the same, showing how the lateral pieces extend over the median and meet at the median-line.

Genus *Soniphilus* Chamberlin

This genus as at present known embraces two species, the one described below and *S. embius* Chamberlin, the type of the genus, a closely related species from Iowa which is but 13 mm. long. In this genus the prehensorial feet are short, not attaining the front margin of the head, and its joints are all unarmed within. The first maxillæ have but one lappet on each side, this being an outgrowth from the proximal article of the palpus. The last ventral plate is very wide. Coxopleural pores few and small, mostly covered by the edge of the ventral plate.

*Soniphilus secundus* sp. nov.

Chitinous lines of prosternum not wholly complete. Claws of prehensorial feet with a minute or obsolete denticle within, not attaining front margin of head. Cephalic plate widest a little in front of caudal margin, narrowing moderately forward. Frontal suture not present. Basal plate very wide. Prebasal plate not exposed. The labrum has two very stout conical teeth at middle, the adjacent processes being abruptly less strongly chitinized and longer like those of lateral fringes. Spiracles all circular, the first larger than the second. First legs a little shorter and more slender than the second. Last ventral plate very wide, narrowed caudad. Two moderate sized pits on each coxopleura covered, or mostly so, by edge of last ventral plate. Anal legs in female slender, longer than the penult, ending in a well developed claw. The body is attenuated strongly caudad and less strongly, though considerably, cephalad. Fulvous; head light reddish yellow; antennæ yellow. Length ad 18 mm. Pairs of legs, in female forty-three, male forty-one.

Localities.—Sausalito (author, April, 1911), Pacific Grove (author, July, 1909).

As indicated previously, this species is very close to the type species *S. embius* found in Iowa and Wisconsin; but it differs clearly in the character of the armature of the labrum, in the shape of the cephalic plate, in the larger basal plate and in details of the last ventral plate and the coxopleuræ. The chitinous lines of the prosternum are also less strongly developed.

*Tabiphilus* gen. nov.

This genus is in general structure most clearly allied with the preceding; but it differs in having the edge not twisted ventrad at the middle, the teeth extending caudad as in most genera and not having the middle two quite so strongly differentiated from the others, and clearly in having two long membranous lappets on each of the first maxilla, the distal lappet being clearly longer than the distal article of the palpus. The one species known is larger and has a much larger number of pairs of legs than any one in the two other genera of the family.

*Tabiphilus rex* sp. nov.

Body light ferruginous. Attenuated cephalad and more decidedly caudad. The cephalic plate is truncate anteriorly and also posteriorly; the sides are straight and parallel from the caudal angles forward to the beginning of

the anterior third where they round in mesad to the anterior margin; longer than wide in ratio 17:15. Frontal suture not present. Antennæ three times as long as the cephalic plate; proximal article wide, nearly touching its fellow; ultimate article equalling in length the two preceding taken together. Prebasal plate very slightly exposed. Basal plate three and eight-tenths times wider than the median length of the exposed portion. Claws of prehensorial feet when closed not attaining front margin of head; joints unarmed. Chitinous lines of prosternum strongly developed; prosternum much wider than long (about 4:3). Ventral pores few, in a transverse band in front of caudal margin of sternite. Legs of first pair a little shorter and more slender than those of the second, the succeeding few pairs gradually a little longer and thicker; anterior pairs clearly more robust than the posterior. First spiracle obliquely elliptic, larger than the second which with all the succeeding ones is circular. The last ventral plate is very wide with its sides convex, the caudal margin subtruncate. Coxopleural pores mostly covered, one or two only being partly exposed. Anal legs much stouter and longer than the penult. Pairs of legs, seventy-five. Length about 30 mm.

The type specimen was taken at Claremont by Prof. Baker and is the only specimen of the species seen.

#### Family Schendylidæ

In this family the antennæ are thin and filiform. The labrum is composed of a single piece, the free edge of which is concave and dentate. Mandible with one dentate lamella, which may be divided into three parts, and one pectinate lamella. Suprascutella never present. The ventral pores when present, as they are in all Californian forms, are condensed in a circular or elliptic area.

*Pectiniunguis* is the only genus now known to occur in California; but *Schendyla* is likely to occur. These two genera may be separated as follows:

#### Key to Genera

- a. Claw of second maxilla excavated and pectinate; dental lamina tripartite; coxosterna of first and second maxillæ grown together.

Genus *Pectiniunguis* Bollman

- aa. Claw of second maxilla not excavated on one side and pectinate; dental lamina of mandible entire; coxosterna of first and second maxillæ not grown together.

Genus *Schendyla* Bergsoe and Meinert

#### Genus *Pectiniunguis* Bollman

Labrum entire, deeply incurved, mesally dentate. Mandible with dentate plate in three divisions. Coxosterna of first and second maxillæ fused together. Claw of pallus of second maxillæ concave on mesal side and finely pectinate along the ventral pores in a small circular field in front of caudal margin of sternites. Last ventral plate wide, each coxopleura with two porigerous pits at or beneath edge of ventral plate. Anal legs six jointed, with or without claws.

#### Key to Species

- a. Anal legs without claws.
- aa. Anal legs with claws.

*P. americanus* Bollman

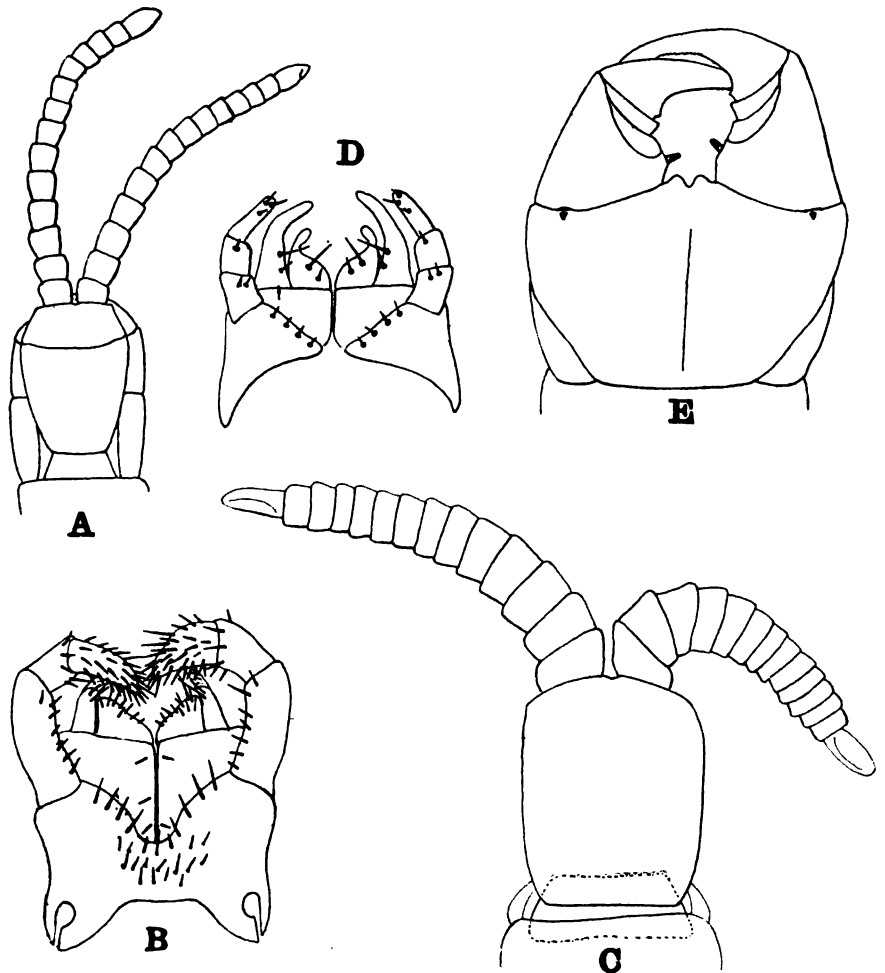


Figure 219

A, Dorsal view of anterior end of *Mecistocephalus limatus* (Wood), showing the characteristic form of cephalic plate and its frontal suture, the narrow basal plate with the pleuræ exposed each side, the much exposed prehensorial feet, and the antennæ. B, First and second maxillæ of the same showing the separation of the coxæ of the first and the long palpus membranous apically and bearing no lappets; note also the extensive fusion of coxæ of second maxillæ. C, Dorsal view of anterior end of *Arrup pylorus* gen. et sp. nov., with the prehensorial feet removed; it shows the cephalic plate with antennæ, the much overlapped basal plate with the pleuræ each side. D, First and second maxillæ of the same, showing particularly the complete separation of the coxæ of the second pair as well as those of the first; contrast with B. E, Prehensorial feet and prosternum of the same; note the characteristic teeth borne on mesal margin of first joint.

- b. Prebasal plate not exposed; pairs of legs, forty-five to fifty-three.
- c. Basal plate, so far as exposed, but four times wider than long; cephalic plate longer than wide. *P. heathi* Chamberlin
- cc. Basal plate very short, exposed portion about eight times wider than long; cephalic plate nearly equal in length and breadth.  
*P. heathi catalinae* subsp. nov.

### *Pectiniunguis americanus* Bollman

While this species has not been taken actually within the state, it was originally described from Lower California and its occurrence within our limits is therefore very probable. In this species the body is depressed and but little attenuated. It is brownish yellow in color with an interrupted geminate dark band along the dorsum. The cephalic lamina is equal in length and breadth, with the caudal margin a little incurved. Prebasal plate exposed. Spiracles large, elliptical. Coxopleural pits covered by last ventral plate. Anal legs entirely without trace of claws. Pairs of legs near sixty-five.

### *Pectiniunguis montereus* Chamberlin

This species seems to occur quite commonly along the California coast from the southern portion north at least as far as Monterey Bay, from which it was first described. It is essentially littoral in habit, though it has been occasionally taken some distance inland. Specimens have been seen from the following localities: Dead Man's Island, San Pedro, (Baker); Santa Barbara, Pacific Grove, etc. (author).

In general structure similar to *P. americanus*. In alcohol specimens are light brown to yellowish with the head somewhat darker. There may be two parallel dark stripes along the dorsum as in the preceding species. In life the adults are deeper colored, some appearing red like a *Linotenia*. The body is decidedly though very gradually attenuated cephalad and more abruptly caudad. The prebasal plate exposed. Cephalic plate considerably longer than wide, truncate caudally. Ultimate article of antennæ shorter than the two preceding taken together. Pairs of legs, so far as noted, fifty-five to sixty-one. Length up to 50 mm.

### *Pectiniunguis heathi* Chamberlin

Body of same general habit as the preceding but smaller. Cephalic plate with sides widely excurving. Prebasal plate not exposed, the cephalic lapping over the basal. Ultimate article of antennæ about equal in length to the two preceding taken together. The first ten sternites have each a caudal median process which fits into a corresponding pit in the succeeding plate, this feature apparently more strongly developed than in *monereus*. Pairs of legs, forty-five to fifty-three. Length 22 mm.

Known from Cypress Point, Monterey County, where a specimen was dug up from an Indian mound in sandy soil, and from Los Angeles, where the author secured a specimen also by digging.

*Pectiniunguis heathi catalinae* subsp. nov.

Head yellowish; antennæ and body pale yellowish white. Cephalic plate widest anteriorly, narrowed caudad; anterior margin rounded, the caudal truncate; equal in length and breadth or very nearly so. Basal plate largely covered by the cephalic, the exposed portion being very short, about eight times wider than long. Claws of the prehensorial feet when closed extending a very little beyond front margin of head; joints of feet all unarmed. Prosternum with chitinous lines; wider than long (about 23:17). Antennæ strictly filiform, not at all attenuated. Last ventral plate wide, sides converging caudad. Coxopleural pits two on each side, covered by edge of ventral plate. Anal legs in male crassate, ending in a claw. Pairs of legs, forty-five to fifty-one: Length about 16 mm.

Localities.—Catalina Island; Claremont (Baker).

## Family Himantariidæ

Antennæ short, strongly flattened, broad at base and markedly attenuated distad. Labrum well developed, composed of a single piece which is free, and incurved and dentate along the margin. Mandible with a single dentate and with several pectinate lamellæ. Prehensorial feet weakly developed, not dentate within. The ventral pores are in a sharply delimited central area. Anal pores never present.

The two genera included in the key below are the only Californian genera at present known; but *Haplophilus*, which is known from Montana and Mississippi, may be found to occur.

## Key to Genera

- a. Anal legs ending in small claws; on some of the middle segments supra-scutella are present. Genus *Notobius* Cook
- aa. Anal legs clawless; no suprascutella present. Genus *Gosiphilus* gen. nov.

Genus *Notobius* Cook

Some of the segments in middle portion of the body with a row of supra-scutella or paratergites above the level of the spiraculiferous sclerites. Labrum deeply incised at median line. Coxosternum of first maxillæ deeply incised at middle, almost completely divided but still coalesced proximally. Last ventral plate very wide; coxopleural pores numerous, small, arranged along edge of ventral plate. Spiracles all circular. Anal legs terminating in a slender claw in adults.

One species known. A second form, *inermis* of Wood, is listed here tentatively.

*Notobius teniopsis* Wood

Syn. *Chomatobius mexicanus* Seliwanoff

*Notobius californicus* Cook

This is a very long species with from one hundred and twenty-nine to one hundred and forty-nine pairs of legs in individuals thus far observed, most having from one hundred and thirty-three to one hundred and forty-one pairs. Con-

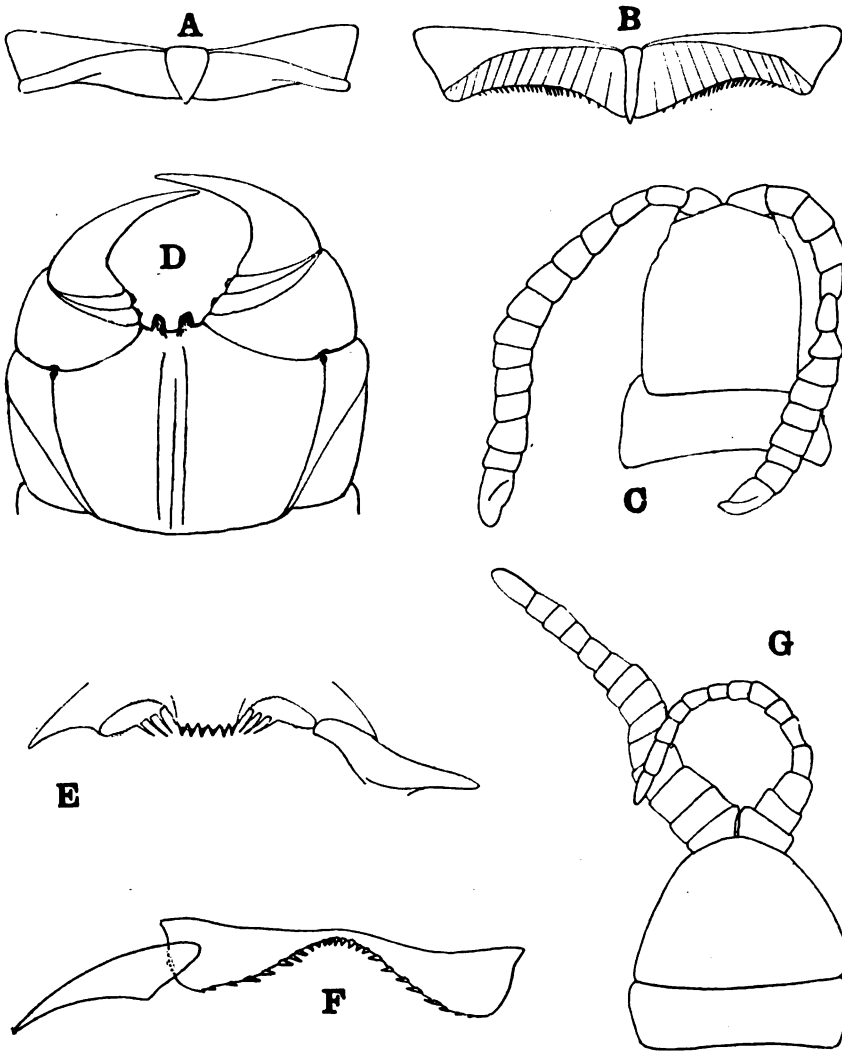


Figure 220

A, Labrum of *Arrup pylorus* gen. et sp. nov. B, Labrum of *Mecistocephalus limatus* (Wood). C, Dorsal view of cephalic and basal plates with antennæ of *Tampiya pylorus* gen. et sp. nov. D, Prosternum and prehensorial feet of the same, showing the characteristic teeth of the anterior median margin of the prosternum. E, Labrum of the same. F, Labrum of *Pectiniunguis montereus* Chamberlin, showing also one lamina fulcientis. G, Dorsal view of anterior end of *Gosiphilus minor* gen. et sp. nov., showing basal and cephalic plates with antennæ, the prehensorial feet being completely covered.

spicuously narrowed from third fourth of length cephalad and abruptly narrowed caudad; the head relatively very small. The cephalic plate is relatively wide, well rounded in front, almost completely concealing the prehensorial feet from above. The flat antennæ are short, contiguous at base and pointed distad. Claw of prehensorial feet not attaining front margin of head. Ventral pores in a sharply delimited median area which varies from circular to transversely elliptical in outline. Last ventral plate very wide, the numerous small coxopleural pores aggregated mostly along its edges.

Specimens have been seen by the author from Stanford, Claremont and Los Angeles. It is also known from San Diego and Margarita Island.

#### *Notobius inermis* Wood.

Under the name *Himantarium inermis*, Wood described an individual from the Santa Cruz Mountains. He states that it is very similar to *teniopsis* but differs in having only one hundred and fifteen pairs of legs. The head is described as triangular and moderately wide, the antennæ short and said not to be acuminate. Feet robust, short.

#### Genus *Gosiphilus* gen. nov.

Body much flattened dorso-ventrally. Labrum deeply incised at middle. The coxosternum of first maxillæ deeply incised at median line but coxæ not separated proximally. Dentate plate of mandible rather narrow. Paratergites or supra-scutella absent. Last ventral plate wide. Coxopleural pores few, mostly covered. Anal legs clawless.

Apparently most closely allied with *Haplophilus*. Established for three species, all of which occur in California and two of them known from nowhere else.

#### Key to Species

- |                                                      |                           |
|------------------------------------------------------|---------------------------|
| a. Pairs of legs near one hundred and eighty-one.    | <i>G. bakeri</i> sp. nov. |
| aa. Pairs of legs less than one hundred.             |                           |
| b. Pairs of legs mostly fifty-five to sixty-one.     | <i>G. minor</i> sp. nov.  |
| bb. Pairs of legs in the neighborhood of eighty-one. | <i>G. laticeps</i> Wood   |

#### *Gosiphilus minor* sp. nov.

Cephalic plate widest caudad, conspicuously narrowed anteriorly, sub-triangular, wholly covering the prehensorial feet; caudal margin weakly produced from lateral corners to a very obtuse angle at middle; much wider than long (as 31:23). Basal plate very wide, narrowed from its anterior end caudad, two and one-half times wider than long. Antennæ short, thick, contiguous at base. Prosternum much wider than long (28:17); chitinous lines very strongly developed. Prehensorial feet weak, joints unarmed, claws not attaining front margin of head. Spiracles all circular, the first considerably larger than the second. Ventral pores in a sharply defined transversely elliptical area. Last ventral plate very wide, almost wholly covering the coxopleuræ, subquadrate, the sides but slightly converging caudad. Coxopleural pores few, partly covered. Anal legs in male



crassate, clavate, the apical portion conspicuously thicker than the proximal. In the female slender, not attenuated distad. Pairs of legs, fifty-five to sixty-one.

Locality.—Berkeley (author, April, 1911).

*Gosiphilus bakeri* sp. nov.

Cephalic plate widest caudad, being a little narrowed cephalad to anterior corners, the border in front of corners triangular; wider than long (in ratio 15:13). Basal plate short, a little narrowed caudad, not quite as wide as the cephalic, about two and eight-tenths times wider than long. Prehensorial feet completely covered by cephalic and basal plates; claws weak, not strongly curved, not touching distally, short of attaining front margin of head. Prosternum very much wider than long (28:15); chitinous lines strongly developed and complete as usual. Spiracles all circular. Ventral pores in a circular or subcircular area just caudad of center of sternites. Last ventral plate wide, sides straight, moderately converging caudad; caudal margin truncate. Coxopleural pits two on each side, the more caudal one partly covered and the anterior one wholly so by ventral plate. Anal legs clawless. Pairs of legs, one hundred and eighty-one.

One specimen from Claremont collected by W. C. Spencer.

*Gosiphilus laticeps* Wood

A long and slender species with the body conspicuously flattened dorso-ventrally. Pairs of legs somewhere near eighty-one, which is a common number. The antennæ are short and conspicuously attenuate distad, contiguous at base. The cephalic plate is wide caudad and strongly narrowed forward. Spiracles small, all circular. Ventral pores in a transversely elliptic area. Last ventral plate wide, sides straight, moderately converging caudad. Coxopleural pores usually, at least, not evident.

Specimens have been examined from Pacific Grove, Claremont, Los Angeles and Catalina Island. It is common in Texas, the type locality, and the author has also secured it at Las Vegas, Nevada, where it was dug up in a garden.





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No. 3

## NOTES ON GEOPHILOIDEA FROM IOWA AND SOME NEIGHBOURING STATES.

BY RALPH V. CHAMBERLIN.

University of Pennsylvania, Philadelphia.

During several weeks in June and July of 1910 I had opportunity for making collections of chilopods in the district indicated by the title of this paper. Unfortunately, the season was unusually dry in these States, particularly in Michigan and Wisconsin, and, as a result, unfavourable for securing an abundance of material. The members of the Geophiloidea seemed especially difficult to uncover; but among the species obtained are several of exceptional interest, two representing new genera, for which it seems necessary to erect a new family. The families of the Geophiloidea now recognized as occurring in the United States, east of the Rocky Mts., may be separated as follows:

- a. Mandibles with a dentate lamella.
  - b. Mandibles with a single pectinate lamella; antennæ filiform or somewhat clavate..... Family *Schendylidæ*.
  - bb. Mandibles with several pectinate lamellæ; antennæ flattened, attenuated distad..... Family *Himantariidæ*.
- aa. Mandibles with no dentate lamella; with a single pectinate lamella.
  - b. Labrum fused for a short distance at middle; antennæ flattened, at least narrowly elliptic in cross-section, attenuated distad..... Family *Sogonidæ*.
  - bb. Labrum entirely free; antennæ cylindrical, filiform or a little clavate.
    - c. Median piece of labrum extending along and, at least in part, fused with the lateral; at middle of free edge with two much larger and more strongly-chitinized teeth directed more or less ventrad..... Family *Soniphilidæ*, fam. nov.
  - cc. Three divisions of labrum distinct; without two such larger and ventrally-directed teeth..... Family *Geophilidæ*.

Of these families, representatives of the Geophilidæ and Soniphilidæ alone were secured in the region covered by this paper. However, the Schendylidæ is represented, *Escaryus urbicus* (Meinert), having been taken in Minnesota, and the same species having been found by the writer to be quite common in New York State. The family Himantariidæ is represented in Texas and Mississippi by a species of Haplophilus, and by at least one of the genus Gosiphilus, *G. laticeps* (Wood). These genera may be found to range into the present section. The family Sogonidæ is at present known to be distributed in Texas (*Timpina texana* Chamberlin, a form with but five joints to the anal legs), and in South Carolina and Tennessee (*Sogona minima* Chamberlin). On the Pacific Coast occur several families not found east of the Rockies.

Family Geophilidæ.

Subfamily Geophilinæ.

Genus Geophilus Leach.

*Geophilus rubens* Say.

Syn. *Geophilus cephalicus* Wood.

*Geophilus lævis* Wood.

*Geophilus okolonæ* Bollman.

Localities.—DeWitt, Mongona and Boone, Iowa ; Franklin Grove, Ill.; Saunder's, Mich.

This is a very common species in Indiana, Ohio and more Eastern States. The form described by Bollman from Arkansas agrees perfectly with this species, excepting that the number of pairs of legs is higher than usual in northern specimens. This, however, is in line with a tendency shown by many other species for the number of legs to show an increase in going from the north to the south or from high elevations to low. It is one of the commonest forms in this district. California specimens also frequently have a larger number of legs.

Genus Arenophilus Chamberlin.

*Arenophilus bipuncticeps* (Wood).

Syn. *Geophilus attenuatus* Bollman (but not certainly of Say).

*Geophilus georgianus* and *latro* Meinert.

*Schendyla perforata* McNeill.

Localities.—Mongona, Boone, DeWitt, Tama, Marshalltown, Iowa ; Fremont, Neb.; Peoria, Ill.; Janesville, Wis.

This is by far the most abundant species. It ranges as a common form through the greater part of the United States in and east of the

Mississippi Valley. At Mongona (June 22), and Marshalltown (June 24), Iowa, and at Sterling, Ill. (June 26), females were taken with recently-laid eggs.

Genus *Pachymerium* Koch.

*Pachymerium ferrugineum* Koch.

Syn. *Geophilus foveatus* (McNeill).

Localities.—DeWitt, Iowa ; Peoria, Ill.; Devil's Lake and Fond du Lac, Wisc.

At Fond du Lac (July 6), the species was found in great abundance among the stones at a river's edge, partly grown individuals being common, and a considerable number of females being found with bodies still coiled about their recently-hatched young.

This is a species widespread in the Eastern United States, as it is in Europe. The specimens secured are similar in size to Austrian specimens, most being under 25 mm. in length.

Subfamily *Chilenophilinæ*

Genus *Taiyuna* Chamberlin.

*Taiyuna opita*, sp. nov.

Proportionately robust ; attenuated strongly caudad, and also decidedly but less strongly cephalad. Sparsely clothed throughout with long bristles.

Head with corners rounded ; sides convexly curving ; caudal margin straight ; anterior margin extended forward from corners to middle, and a little incurved at median line ; longer than wide in ratio, 19:16, and five times longer than exposed portion of basal plate. Prebasal plate absent. Basal plate overlapped in front by the cephalic, and behind by the first dorsal plate ; free portion wider than median length in about ratio 34:7. Antennæ short ; articles moderate and short, the ultimate equal in length to the two preceding taken together.

Claws of prehensorial feet when closed reaching the distal end of the first antennal article. Claw at base with a subcylindric, apically truncate, tooth ; prefemur also with a strongly chitinized tooth at distal end ; the intermediate joints also each with a distinct, conical and well-chitinized tooth. Prosternum unarmed ; its anterior median margin nearly straight, not excised ; chitinous lines not evident ; suture parallel with margin ; wider than long in ratio 39:35, longer than prefemur in ratio 7:4. Dorsum weakly bisulcate, also with a more median pair of fine sulci. Anterior præscuta short, being of moderate length in the middle region, and then

again shortening caudad. Spiracles all circular, the first greatly exceeding the second in size. First pair of legs much reduced; anterior pairs more robust than the caudal, not shorter. Anterior ventral plates with a rather weak median sulcus, most plates plane; pores not detected. Last ventral plate moderately wide; margins straight, the lateral moderately converging caudad. Coxopleuræ with about four pores in a row under edge of plate, and four or five free on the sides, well separated from each other. Anal legs longer and more crassate than the penult; without claws. Pairs of legs (in female) 41.

Length of female 15 mm.; width .9 mm.

Localities.—Posers and Kimball's, Mich.

Genus *Gnathomerium* Ribaut.

*Gnathomerium umbraticum* (McNeill).

Syn. *Gnathomerium americanum* Ribaut.

Locality.—Manitou, Colorado.

This seems to be a southern species, occurring widely and abundantly throughout the Southern States. In favourable seasons it may be found to be not rare in the present region, as Bollman reports it as common in Indiana.

Subfamily Linoteniinæ.

Genus *Linotenia* Koch.

*Linotenia chionophila* (Wood).

Localities.—Devil's Lake and Ashland, Wis.

Many specimens were taken at the former locality under leaves and stones about the margin of the lake. This species is boreal, being abundant, comparatively, in Alaska and adjacent islands. It was first described from specimens taken at Fort Simpson on the Red River of the North. It is very close to *Linotenia acuminata* (Leach) of Europe, and may have to be merged with it.

*Linotenia fulva* (Sager).

Localities.—Mongona, Boone, DeWitt and Marshalltown, Iowa; Franklin Grove, Ill.; Sterling, Ill.

Very much the commonest *Linotenia* in the Northern United States, and one of the commonest members of the entire order.

Family Soniphilidæ, fam. nov.

Genus *Soniphilus*, gen. nov.

Labrum free; the median part firmly fused to the lateral, at least at ends; edge of median portion directed ventrad and bearing a number of

very stout teeth, which extend directly ventrad (the figure accompanying suggests a bedding of these teeth somewhat caudad, which does not exist); of these teeth the two median are clearly largest, the others decreasing from median to outermost; lateral portions with edge bearing a few spinous processes much more weakly chitinized than the teeth of middle portion. (See pl. 1, fig. 3.) Mandibles with a single pectinate lamella; no dentate lamella. Both branches of first maxillæ set off by a suture; the outer branch biarticulate, entirely without lappets or with a single short, conical one on outer edge of base; coxæ completely fused at mesal line. Coxæ of second maxillæ fused at middle; palpi short, bearing a simple claw of normal size.

Chitinous lines of prosternum strongly developed. Prehensorial feet with joints all unarmed; claws when closed not attaining front margin of head. Frontal plate not discrete. Prebasal plate absent. At least the anterior sterna with caudal margin strongly chitinized in a sharp edge or blade-like form, which fits into a transverse groove in anterior margin of succeeding plate. (See fig. 5.) Pores not detected. Dorsal plates bisulcate. Last ventral plates very wide. Anal legs six-jointed, ending in claws.

Type.—*Soniphilus embius*, sp. nov.

*Soniphilus secundus* Chamb., a Californian species, also belongs here.

*Soniphilus embius*, sp. nov.

Slender, attenuated cephalad and caudad; body very sparsely provided with short straight hairs, the head with longer ones.

Yellowish-white, the anterior region more strongly yellow or lemon colored; head with prosternum and prehensorial feet pale reddish brown; antennæ yellowish white.

Head widest over caudal portion, the sides from middle caudad but very slightly converging, the sides in front of middle nearly straight and clearly converging; anterior margin with middle part straight, transverse, on each side a little oblique, extending a little caudad in running from middle to lateral cornea, straight. Frontal suture absent. Prebasal plate absent. Basal plate four times as wide as its median length, a little wider than cephalic plate (24:23). Antennæ filiform, of moderate length; articles longer than wide, decreasing in length distad to the penult, the ultimate about equal in length to the two preceding taken together.

Claws of prehensorial feet when closed not attaining the anterior margin of head, short, the inner free margin of prefemur very short or



almost obliterated ; claw within a very small conical tooth at base, other articles unarmed. Prosternum with chitinous lines well developed ; two submedian longitudinal sulci ; anterior margin unarmed, weakly angularly depressed from sides to median line ; much wider than long (14:9), longer than greatest length of prefemur nearly in ratio 9:5. Dorsum weakly bisulcate. Prescuta of middle region moderate or short, not much decreasing in length cephalad and caudad. Spiracles all circular, relatively large, the first considerably larger than the second, the others gradually decreasing from the second caudad. Legs of first pair decidedly shorter and more slender than the second. Ventral pores not detected. Plates of anterior portion of body with a transverse groove along cephalic edge, which is protected by a flange-like extension on the ventral side ; into this groove fits the well-chitinized, extended blade-like caudal edge of the preceding plate in each case. Last ventral plate very wide, strongly narrowed caudad, the lateral margins a little incised below middle ; caudal margin straight. Coxo-pleuræ each with a single free isolated pore of small size, and two larger pits covered by the edge of the plate. (See fig. 4.) Anal legs longer and slightly stouter than the penult (female). Pairs of legs (female) 43.

Length, 13 mm.

Localities.—DeWitt, Iowa.

The type is a single female, which was taken with her recently-laid eggs.

Genus *Poaphilus*, gen. nov.

Agreeing in general with *Soniphilus*, as described above, but readily distinguished in having the joints of the prehensorial feet dentate within and its claws extending much beyond the front margin of the head. The last ventral plate is narrow or but moderate in width, not very wide, as in the preceding genus.

Type.—*Poaphilus kewinus*, sp. nov.

Aside from the species here described, a second one from New Mexico is also known.

*Poaphilus kewinus*, sp. nov.

Body very small, strongly attenuated cephalad and caudad.

Antennæ and legs pale yellow ; body light yellowish brown ; head with prosternum and prehensorial feet light reddish brown.

Head much longer than wide (11:8) ; ten or eleven times as long as the very short basal plate ; relatively narrow, leaving sides of prehensorial

feet exposed for entire length ; caudal margin truncate, sides weakly bowed outward from end to end, the anterior margin rounded on each side, mesally incised. Frontal plate not discrete. Prebasal plate absent. Basal plate greatly abbreviated, the exposed portion eight times as wide as long.

Antennæ filiform, as compared with body length rather long ; articles moderately long, decreasing distad, the ultimate a little longer than the two preceding together ; bristles very long, distad, becoming shorter and denser as usual.

Claws of prehensorial feet when closed attaining distal end of first antennal article ; claw armed at base with an acute conical tooth, prefemur with a low, conical and subdentiform protrusion on mesal surface, other joints unarmed. Prosternum wider than long in ratio 20:17 ; longer than the prefemur in the ratio 17:10, nearly ; chitinous lines distinct. Dorsal plates bisulcate ; also with a weak median sulcus. All prescuta short. All spiracles circular, the first larger than the second. First pair of legs shorter and much more slender than the second ; anterior pairs shorter and thicker than those of posterior portion of body. Last ventral plate moderately wide, narrowed caudad, the margins nearly straight, the caudal slightly excised. Coxopleural pores four, small, two of these covered or partly covered by the edge of the last ventral plate and the other two free. Anal legs longer and thicker than the penult, ending in a long slender claw. Pairs of legs in female, 37.

Length, 6.5 mm.

Locality.—Marshalltown, Iowa.

The type, as with the preceding species, is a single female which was taken—her eggs were very few in number.

#### EXPLANATION OF PLATE.

*Soniphilus embius*, gen. et sp. nov.

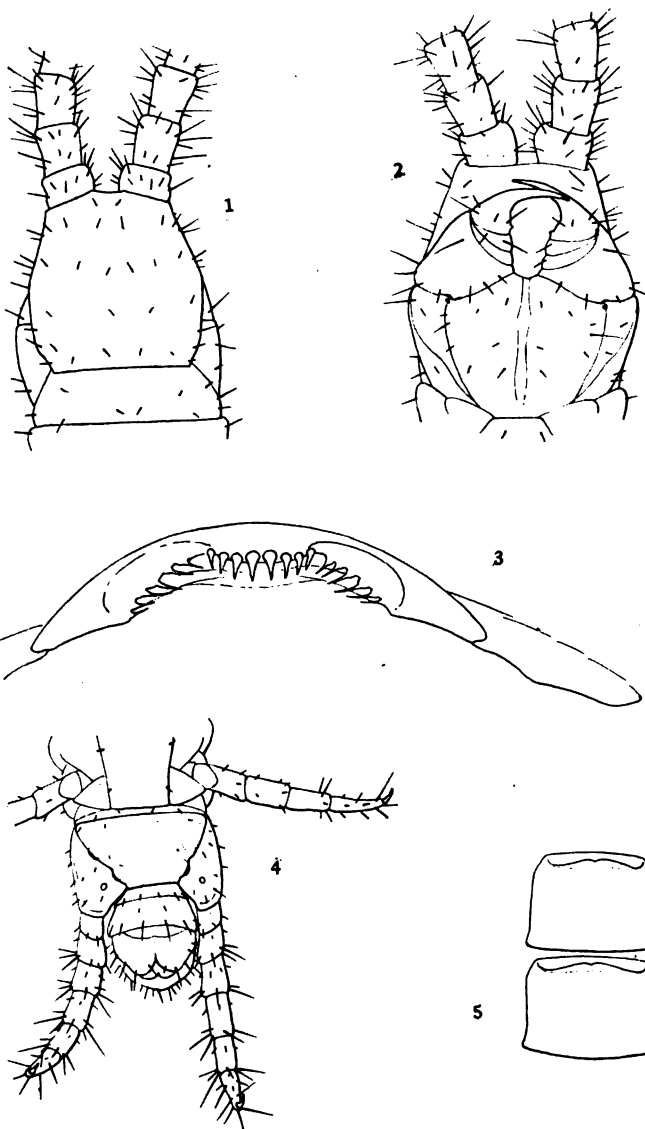
Fig. 1.—Dorsal view of anterior portion.

Fig. 2.—Ventral view of anterior portion.

Fig. 3.—Labrum, ventral aspect. (The teeth of median portion normally extend directly ventrad ; the figure shows them extending caudo-ventrad, this resulting from depression by the cover-glass).

Fig. 4.—Ventral view of posterior portion.

Fig. 5.—Ninth and tenth ventral plates.



SONIPHILUS EMBIUS, GEN. ET SP. NOV.

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**THE GEOPHILOIDEA OF THE SOUTHEASTERN STATES.**

**BY RALPH V. CHAMBERLIN.**

**WITH THREE PLATES.**

**CAMBRIDGE, MASS., U. S. A.:  
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APRIL, 1912.**



No. 13.— *The Geophiloidea of the Southeastern States.*

BY RALPH V. CHAMBERLIN.

OUR knowledge concerning the Chilopoda of the southeastern section of the United States has long been so meager and fragmentary, that it is considerable satisfaction to present a revision of the Geophiloidea of the region based upon the study of rather extensive material. Most of this material was secured by the author himself through systematic collecting carried out during the summer of 1910, every section of the region being visited excepting southern Florida (which, as belonging rather to another fauna, is not included) and the coastal portions of Georgia and the Carolinas. It has been possible to ascertain somewhat clearly the limits of distribution of a number of important species together with the range and directions of their variations and thereby to bring about simplification through the relegation to synonymy of many names given to forms of non-specific grade. All the species previously recorded from the region were secured, as well as representatives of a number of undescribed ones, among which are the types of two genera for which it seems necessary to erect a new family. Of importance, also, was the rediscovery of Bollman's *Scolioplanes gracilis*, later made the type of the genus *Agathothus*, the affinities of which have for twenty years been in doubt, no diagnosis having heretofore been published.

Dr. Meinert's types of North American species in the collection of the Museum of Comparative Zoölogy have been available for study and comparison during the preparation of this paper. The types of the new species are also in the collection of the Museum.

The following list is introduced by way of summary; synonyms are printed in italics.

**GEOPHILIDAE.**

**GEOPHILINAE.**

**POLYCRICUS** Humbert and Saussure.

*P. floridanus* Cook = *P. marginalis* (Meinert).

*P. marginalis* (Meinert).

**PACHYMERIUM C. L. Koch.**

*P. ferrugineum* (C. L. Koch).

*P. foveatum* (McNeill) = *P. ferrugineum* (C. L. Koch).

**ARENOPHILUS, gen. nov.**

*A. attenuatus* (Say) = ? *bipuncticeps* (Wood).

*A. bipuncticeps* (Wood).

*A. georgianus* (Meinert) = *A. bipuncticeps* (Wood).

*A. latro* (Meinert) = *A. bipuncticeps* (Wood).

*A. perforatus* (McNeill) = *A. bipuncticeps* (Wood).

*A. unaster* Chamberlin.

*A. watsingus*, sp. nov.

**GEOPHILUS Leach.**

*G. atopleurus* Chamberlin = *G. mordax* Meinert.

*G. cephalicus* Wood = *G. rubens* Say.

*G. huronicus* Meinert.

*G. laevis* Wood = *G. rubens* Say.

*G. lanius* Brölemann = *varians* McNeill.

*G. legiferens* Chamberlin.

*G. louisianae* Brölemann = *mordax* Meinert.

*G. mordax* Meinert.

*G. rubens* Say.

*G. salemensis* Bollman = *G. mordax* Meinert.

*G. varians* McNeill.

*G. virginensis* Bollman = *G. mordax* Meinert.

**CHILENOPHILINAE.****WATOPHILUS, gen. nov.**

*G. alabamæ*, sp. nov.

**GNATHOMERIUM Ribaut.**

*G. americanum* Ribaut = *G. umbraticum* (McNeill).

*G. umbraticum* (McNeill).

**LINOTENIINAE.**

LINOTENIA C. L. Koch.

- L. bidens (Wood).
- L. bothriopa (Wood) = L. fulva (Sager).
- L. branneri Bollman.
- L. chionophila (Wood) = ? branneri Bollman.
- L. fulva (Sager)
- L. robusta (Meinert) = L. fulva (Sager).
- L. ruber Bollman = L. bidens (Wood).

AGATHOTHUS Bollman.

A. gracilis Bollman.

**SOGONIDAE**, fam. nov.

SOGONA, gen. nov.

S. minima, sp. nov.

TIMPINA, gen. nov.

T. texana, sp. nov.

**HIMANTARIIDAE.**

GOSIPHILUS Chamberlin.

G. laticeps (Wood).

HAPLOPHILUS Verhoeff.

H. grenadae, sp. nov.

The families recognized as occurring in the region may be separated by means of the following key.

*Key to families.*

- a. Mandibles with a single pectinate lamella, and with no dentate lamella.
- b. Antennae flattened, attenuated distad; labrum of one piece which is fused mesally and free laterally. *Sogonidae*, fam. nov.



- bb. Antennae filiform or somewhat clavate; labrum tripartite, entirely free. *Geophilidae.*
- aa. Mandibles with one dentate lamella and with several pectinate lamellae. *Himantariidae.*

### GEOPHILIDAE.

This large family as represented in the southeastern states embraces three subfamilies: — the Geophilinae, including the genera Polycricus, Pachymerium, Arenophilus, gen. nov., and Geophilus; the Chileno-philinae, including Watophilus, gen. nov. and Gnathomerium; and the Linoteniinae, including the genera Linotenia and Agathothus. These groups and genera, so far as affects the species here dealt with, may be separated as follows.

#### *Key to subfamilies and genera.*

- a. Median piece of labrum very large, armed with a fringe of teeth or spines; lateral pieces small, free edge smooth, unarmed. *Linoteniinae.*
- b. Claw of prehensors unarmed; conspicuously excavated at proximal end dorsally, constricted. *Agathothus* Bollman.
- bb. Claw of prehensors armed within with a single large tooth; not excavated proximally. *Linotenia* Koch.
- aa. Median piece of labrum relatively very small, the lateral pieces large and with the free edge armed with few to many spinescent processes.
  - b. Second maxillae with a very strongly chitinized oblique, pleurosternal suture. *Chilenophilinae.*
  - c. Middle piece of labrum completely separating the lateral; anal legs clawless, with seven articles beyond coxopleura. *Watophilus*, gen. nov.
  - cc. Middle piece of labrum not separating the lateral; anal legs armed with claws, having six articles beyond the coxopleura. *Gnathomerium* Ribaut.
  - bb. Second maxillae without any such chitinous suture. *Geophilinae.*
  - c. Prehensorial feet mostly not extending beyond anterior margin of head, the joints unarmed within or only obscurely so (last ventral plate mostly wide to very wide). *Geophilus* Leach.

- cc. Prehensorial feet much exposed from above, extending well beyond anterior margin of head, the joints distinctly denticulate within; (last ventral plate either wide or narrow).
- d. Last ventral plate very wide; coxopleural pores aggregated and opening into two large pits on each side adjacent to or covered by edge of last ventral plate; anal legs clawless, composed of seven articles beyond coxopleura.  
*Arenophilus*, gen. nov.
- dd. Last ventral plate narrow; pores of coxopleura not aggregated and opening into pits; anal legs with six joints beyond coxopleura (with or without claw).
- e. Ventral pores in four areas, two on anterior portion of plate and two on posterior; (anal legs in ours clawless).  
*Polycricus* Humbert and Sausurre.
- ee. Ventral pores not in four areas in this way; anal legs with claws.  
*Pachymerium* Koch.

#### GEOPHILINAE.

#### GEOPHILUS Leach.

Trans. Linn. soc. London, 1814, 11, p. 384.

The species recognized as occurring in the southeastern states may be separated by means of the following key.

#### Key to species.

- a. Frontal plate discrete.
  - b. Prebasal plate exposed.
    - c. Coxopleurae of last pediferous segment with two large pits which are covered by the last ventral plate. *G. rubens* Say.
    - cc. Coxopleurae of last segment with from five or six to many small pores. *G. mordax* Meinert.
  - bb. Prebasal plate not exposed.
    - Pairs of legs — sixty-one or close thereto.  
*G. legiferens* Chamberlin.
- aa. Frontal plate not discrete.
  - b. Prebasal plate not exposed.
    - c. Last ventral plate wide. *G. huronicus* Meinert.
    - cc. Last ventral plate narrow. *G. varians* McNeill.

## GEOPHILUS RUBENS Say.

Journ. Acad. nat. sci. Phil., 1821, 2, p. 21.

*Geophilus cephalicus* Wood, Journ. Acad. nat. sci. Phil. 1862, ser. 2, 5, p. 44.

*Geophilus laevis* Wood, ibid. Trans. Amer. philos. soc., 1865, new ser., 13, p. 180.

*Strigamia rubens* Wood, Trans. Amer. philos. soc., 1865, new ser., 13, p. 182.

LOCALITIES.— Virginia, near Washington, D. C.; Raleigh, N. C. (seq. Brölemann).

Contrary to the usual supposition, this species, so abundant in the more northern states, is very rare in the greater part of the South, or, rather, wholly absent.

## GEOPHILUS MORDAX Meinert.

Proc. Amer. philos. soc., 1886, 23, p. 218.

*Geophilus salemensis* Bollman, Entom. Americana, 1887, 3, p. 82.

*Geophilus virginiensis* Bollman, Proc. U. S. N. M., 1889, 11, p. 346.

*Geophilus louisianae* Brölemann, Ann. Soc. ent. France, 1896, 65, p. 55.

*Geophilus atopleurus* Chamberlin, Ann. Ent. soc. America, 1909, 2, p. 181.

LOCALITIES.— Watervalley, Holly Springs, Grenada, Gulfport and Longbeach, Miss.; Louisiana; Maplesville and Thomasville, Ala.; Raleigh, Marion, Salisbury, and Hot Springs, N. C.; Unaka Springs, Tenn.; Virginia, near Washington, D. C.

This is a common and conspicuous species in the Southern States, where it appears to replace *G. rubens* Say of the states farther north, a species probably very closely related. The present species is subject to considerable variation in size, coloration, and in the number and arrangement of the pleural pores though the latter uniformly present certain distinctive features. Typically, the individuals of this species are in life distinctly red, the coloration being almost precisely that of many or most Linotenias, such as *L. fulva* and *L. bidens*. Occasionally the red is less dense, the color being pinkish or the more ordinary yellowish brown. In alcohol the red color quickly fades. The

characteristic structure of the head and prehensorial feet and the conspicuous pits at cephalic edge of the anterior sterna with the corresponding processes of the caudal margins are features by which the species may readily be recognized when taken in connection with the shape of the last ventral plate and the nature of the coxopleural pits. Mr. Bollman established *G. virginiensis* chiefly on the presence of these sternal pits in his type; but he must not have had specimens which he recognized as *G. mordax*, for the type of this species, which I have recently examined, together with all the other specimens studied, have these pits plainly showing, though in some few they are less conspicuous and may be overlooked when the sterna are closely articulated. Mr. Bollman also suggests a difference in the proportions of the "coxa" of the prehensorial feet. As to *mordax*, Meinert says: "sternum... sesqui latius quam longius, coxa fere duplo longius (20:11)." Mr. Bollman appears uniformly in constructions corresponding to this in Meinert's various descriptions to have taken the *longius* as being in agreement with coxa; but plainly the comparison is between length of sternum and that of coxa, not between length and breadth of the latter. A cotype of *G. salemensis* which I have examined is also a large specimen of *mordax* in which the sternal pits are conspicuously developed though they appear to have been overlooked by Mr. Bollman.

Of the coxopleural pores one is typically somewhat larger than the others and more or less isolated on the more caudal portion of the coxopleurae, the others being cephalad of it. In medium sized individuals the pores are usually scattered over the surface of the coxopleurae; but with increasing age there is a distinct tendency for the pores to become crowded along the edge of the ventral plate in mostly two rows and similarly along the dorsal plate, leaving the greater portion of the coxopleural surface free from pores excepting for the single isolated one. Often the ventral pores, excepting this single one, become shifted entirely beneath the edge of the ventral plate and the dorsal ones similarly beneath the dorsal plate. At the same time there is a tendency for some pores to close up and disappear in later moults, so that there results a progressive reduction in the number of pores. Brölemann's *G. louisianae* is clearly based upon an old individual of *mordax* in which the pores are thus somewhat reduced in number and covered by the ventral plate excepting for the single one. In a few individuals, quite old as judged by the appearance of the head, which have been studied there appears a tendency for the isolated pore to become reduced and then closed. In the form described by

the writer as *atopleurus* there is no single pore but in its place a peculiar chitinous thickening that at first appears like a minute tooth or spine. In a number of additional specimens in this condition taken in Mississippi, the characteristics upon which the original was separated as a species are well marked. The chitinous marks are in shallow depressions and after a careful study of them, I conclude that they represent the completely closed pores, the lines being the appressed and fused margins of the pore. This condition appears to be rare.

There is considerable variation in the anal pores, these being usually less readily distinguishable in older individuals than in young and partly grown ones. In fact, they seem in some old specimens to have become grown over and closed. Hence the possibility of Meinert's statement "*Pori anales nulli.*" In the great majority of individuals, however, the pores are distinct, though often not readily seen from ventral view.

*GEOPHILUS LEGIFERENS* Chamberlin.

Ann. Ent. soc. America, 1909, 2, p. 182.

LOCALITY.—Virginia, near Washington, D. C.

*GEOPHILUS HURONICUS* Meinert.

Proc. Amer. philos. soc., 1886, 23, p. 220.

LOCALITY.—Russellville, Tenn.

A northern species. The specimens from Russellville agree in all essential points with Meinert's types, with which they have been directly compared. The next species, *varians*, is at least very close also, the main difference being in the last ventral plate which is much narrower than that of typical *huronicus*.

*GEOPHILUS VARIANS* McNeill.

Proc. U. S. N. M., 1887, 10, p. 332.

*Geophilus lanius* Brölemann, Ann. Soc. ent. France, 1896, 65, p. 51.

LOCALITIES.—Raleigh, N. C. (Brölemann); Indiana.

Only the type specimens known.

POLYCRICUS Humbert and Saussure.

Etudes sur les Myriop., 1872, p. 143.

One species within our range apparently referable to this genus is known from Florida.

POLYCRICUS MARGINALIS (Meinert).

*Geophilus marginalis* Meinert, Proc. Amer. philos. soc., 1886, 23, p. 218.

*Polycricus floridanus* Cook, Proc. Ent. soc. Washington, 1899, 4, p. 307.

LOCALITIES.— Key West, type locality and Miami (J. H. Comstock), Fla.

The specimen from Miami agrees fully with Meinert's type.

PACHYMERIUM C. L. Koch.

Syst. d. Myriopoden, 1847, p. 85 and 187.

PACHYMERIUM FERRUGINEUM (C. L. Koch).

*Geophilus ferrugineus* C. L. Koch, Deutsch. Crust. Myr. Arach., 1835, 3, p. taf. 2.

*Mecistocephalus foveatus* McNeill, Proc. U. S. N. M., 1887, 10, p. 333.

*Geophilus attenuatus* Cook (nec. Say), Proc. U. S. N. M., 1895, 18, p. 59.

LOCALITIES.— Holly Springs and Watervalley, Miss.; New Orleans, La.; Jackson, Ala.; Asheville, N. C.

A female with very recently hatched young was taken, among numerous specimens, at Asheville on Aug. 6. Apparently, however, most of the females, at this place, leave their young considerably earlier in the season, many young being found some way along in development.

While the species is often found under bark of trees and beneath leaves, I have taken it by far in greater numbers under stones along river courses. At New Orleans it was found very abundant in a vacant lot upon which there were piles of stones and pieces of bricks, beneath which it occurred. At Wisconsin it was found early in July in great abundance under stones and gravel at the edge of a

stream, females with young still in the nest, partly grown young as well as many isolated adults being taken. This seems a favorite location for them, at any rate during the summer season.

This is a wide-spread species in the northern as well as in the southern states; but in the latter region it is by no means so common as *A. bipuncticeps*, *G. umbraticus*, *G. mordax*, or even *A. watsingus*. Where found, however, a considerable number of specimens were usually secured, the individuals almost swarming in several limited areas. The specimens secured are all small, like those of Austria-Hungary as described by Dr. Latzel; they vary from 15 to 35 mm. in length with but few approaching the upper limit, the greater number by far being under 25 mm. The number of legs in the specimens that were examined for this feature ranged from 41 to 47 pairs.

**ARENOPHILUS, gen. nov.**

Prebasal plate not evident; frontal suture absent. Basal plate trapeziform, strongly narrowed cephalad.

Labrum, free, tripartite; the middle piece fully separating the lateral, armed with a series of small teeth or teeth-like processes; the lateral pieces with a fringe of numerous long, slender spinescent bristles or processes.

First maxillae nearly as in *Geophilus*; the coxae completely fused at middle and separated from distal divisions by suture; palpi, biarticulate, coxae and femora with long membranous lappets at distal external angles.

Second maxillae without pleurosternal sutures; palpus triarticulate, without processes at distal end of femur.

Coxosternum of prehensors without chitinous lines or but weakly indicated. Prehensorial feet large, much exposed from above, extending cephalad well beyond anterior margin of head; articles distinctly denticulate within.

Ventral pores condensed, in definite areas, numerous.

Last ventral plate, wide. Coxopleural pores aggregated and opening into two large pits on each side which are mostly covered in whole, or in part, by the last ventral plate.

Anal pores present.

Anal legs unarmed; at distal end a very small seventh article.

TYPE.—*Geophilus unaster* Chamberlin.

Three species from the present region are referable to this genus. They may be separated as follows.

*Key to species.*

- a. Ventral pores in a median longitudinal lanceolate area, the apex cephalad. *A. unaster* Chamberlin.
- aa. Ventral pores not in a median longitudinal lanceolate area.
- b. Ventral pores in a transverse area extending across the plate, or nearly so, in front of caudal edge. *A. bipuncticeps* (Wood).
- bb. Ventral pores in a median circular or subcircular area. *A. watsingus*, sp. nov.

*ARENOPHILUS UNASTER* Chamberlin.

Ann. Ent. soc. America, 1909, 2, p. 179.

LOCALITY.—Austin, Texas (J. H. Comstock and T. H. Montgomery, coll.).

While not actually taken within the region strictly covered by the present paper, it is likely to occur and is introduced in the key for purposes of comparison with *A. bipuncticeps*, and others, with which it is very closely related and perhaps cognate, *A. watsingus* also bearing a similarly close relation. *G. aster* is a large form conspicuously different from these related forms in the arrangement of the ventral pores. These occur on the anterior ventral plates in the form of a lanceolate area with the point cephalad, the area extending from the caudal margin the greater distance across the plate. All Texas specimens which I have seen are very constant in this character. *A. unaster* appears completely to replace *bipuncticeps* and *watsingus* in this region where it seems to be abundant.

*ARENOPHILUS BIPUNCTICEPS* (Wood).

*Geophilus bipuncticeps* Wood, Journ. Acad. nat. sci. Phil., 1862, ser. 2, 5, p. 45. Trans. Amer. philos. soc., 1865, new ser., 13, p. 180.

? *Geophilus attenuatus* Say, Journ. Acad. nat. sci. Phil., 1821, 2, p. 114. Bollman, Proc. U. S. N. M., 1889, 11, p. 347; Bull. 46, U. S. N. M., 1893, p. 14.

*Geophilus georgianus* Meinert, Proc. Amer. philos. soc., 1886, 23, p. 219.

*Geophilus latro* Meinert, Myr. Mus. Haun., 1871, 1, p. 79.

*Schendyla* ? *perforatus* McNeill, Proc. U. S. N. M., 1887, 10, p. 325.



LOCALITIES.—Holly Springs, Byram, Fernwood, Hudsonville, Grenada, Canton, Jackson, Biloxi, Ocean Springs, Longbeach, Gulfport, Miss.; Selma, Jackson, Birmingham, Anniston, and Mobile, Ala.; Lula, Ga.; Russellville, Tenn.

The ventral pores in this species are numerous and conspicuous. They are arranged in a transverse area extending entirely across the plate immediately in front of the caudal margin, the area being mostly in the form of a very low triangle with the apex caudad; more rarely, it is in the form of an elongate, narrowly diamond-shaped area. This character may be detected even in very young specimens.

The type of *G. georgianus* I find to be a medium sized female agreeing fully with *bipuncticeps*. Meinert is in error in saying no anal pores are present. The anal pores in grown individuals are usually to be seen well only in lateral view. The opening lies in a depression and varies considerably in size, and, because of expansion of the canal, more so in appearance than in actuality, sometimes appearing very large where the tegument is transparent. *A. latro* of Meinert is based upon an individual in which the pores appear large, but it seems clearly this species. In other cases the folding of the tegument may so cover the pores that they are detected with difficulty and might be supposed to be absent (*A. georgianus* Meinert). Of *A. latro* I have not seen the original types; but in the Museum of Comparative Zoölogy there are four specimens determined by Meinert which are doubtless equally authentic.

ARENOPHILUS WATSINGUS, sp. nov.

Strongly attenuated caudad, less strongly cephalad; in general very sparsely provided with straight hairs which are moderate to long.

Body and legs yellow, the antennae a little darker. Head and prehensorial feet with prosternum light reddish brown. Cephalic plate much longer than wide (31:22), six times longer than the exposed portion of the basal plate in type specimens, but varying somewhat in others; subtruncate anteriorly and posteriorly, the sides nearly straight excepting at anterior and posterior ends where they bend obliquely mesocephalad and mesocaudad respectively, the caudal oblique portion being longer than the anterior. Frontal plate not discrete. Cephalic plate on caudal portion with two long sulci which run cephalad from caudal margin and diverge a little; glabrous or nearly so, there being a very few bristles (see Plate 1, fig. 1). Exposed portion of basal plate at middle considerably more than

four times as wide as long (4.4:1), being considerably overlapped by cephalic plate, at sides the length  $\frac{1}{2}$  the width (Plate 1, fig. 2).

For labrum see Plate 1, fig. 4. Lappets of first maxillae large, membranous.

Antennae long to very long, all articles long excepting a few before the ultimate; ultimate article clearly shorter than the two preceding together (5:4); most articles clothed with a limited number of long straight bristles subdefinitely arranged, the distal articles becoming densely clothed with finer, shorter, straight hairs.

Claws of prehensorial feet when closed extending much beyond cephalic margin of head but not fully attaining the distal end of first antennal article. The claw with a small, subcylindrical, blunt tooth at base; first joint with a very low, obtuse denticule; other joints and prosternum unarmed. Prosternum with anterior mesal margin widely but only weakly sinuate; subquadrate; wider than long in about ratio 20:17, considerably less than twice as long as the coxa (32:21); coxopleural suture subparallel with lateral margin, curving mesad a little in going caudad. Chitinous lines very weak and indistinct. Prosternum and prehensorial feet both almost glabrous, bearing a few long, scattered bristles (Plate 1, fig. 1).

Anterior prescuta short, becoming long in middle and posterior regions.

Anterior spiracles moderately large, the first considerably longer than the second, broadly elliptic, a few following subsimilar, but nearly all circular, the ultimate ones becoming small.

Ventral pores in a rather large circular to somewhat quadrate or broadly diamond-shaped area on median caudal portion of plate; in front of poriferous area a median sulcus extending toward anterior margin, this crossed a little cephalad of its caudal end by a number of transverse lines.

First pairs of legs shorter and much more slender than the second; anterior legs clearly more robust than the posterior pairs but of about equal length; legs very sparsely hirsute.

Last ventral plate very wide, all margins straight or the caudal a little indented mesially with its lateral portions a little convex, the lateral margins not strongly converging caudad. Coxopleurae moderately enlarged; each with two pits which are usually covered or mostly so by the last ventral plate.

Anal pores concealed.

Anal legs in the male much longer than the penult, crassate, the ultimate articles less so than the proximal; no claw, there being in its

place a very small, pilose process resembling a diminutive additional article (Plate 1, fig. 2); in the male sparsely clothed with long bristles and densely with finer short hairs; in the female the legs are also crassate but less strongly so than in the male and they are more uniform in thickness.

Pairs of legs in male 33-59; in female 53-63.

Length of type male 27 mm.; width ad. 9 mm.

LOCALITIES.—Chatham, Va.; Landrum, Seneca and Taylor's, S. C.; Hot Springs and Brown's Summit, N. C.; Lexington and Fulton, Ky.; Gainesville, Lula, Tallulah Falls, and Atlanta, Ga.; Anniston, Ala.; Watervalley, Miss.

The specimens described are mainly from Chatham, Va. The specimens from this and several other of the more northerly locations seem to have the number of pairs of legs almost fixed at 53 in both male and female; but in those from other localities, such as Seneca, S. C., the mode is higher although the specimens otherwise agree closely. As previously indicated this species is very close to *bipuncticeps* and the large individuals except upon critical examination are scarcely to be distinguished; this is shown by the fact that they seem always heretofore to have been confused with that species. In many places both *bipuncticeps* and *watsingus* may be secured in the same area; but usually one will be found to prevail to the exclusion of the other. In many places toward the north of our range, *watsingus* seems wholly to replace *bipuncticeps*, while in other large areas the latter alone occurs. In Illinois, Iowa, etc., *watsingus* does not occur, *bipuncticeps*, on the other hand, being there much the commonest geophilid.

#### CHILENOPHILINAE.

##### WATOPHILUS, gen. nov.

Frontal suture not evident. Prebasal plate absent. Dorsal plates bisulcate.

Labrum free, tripartite, the middle piece fully separating the lateral and armed along the free edge with a row of small spines or spine-like teeth; the lateral pieces with fewer, larger processes, or spines.

First maxillae with coxae completely fused at middle, separated by suture from distal divisions; palpus biarticulate, the coxa and femur on outer side with very long membranous lappets.

Second maxillae with strongly developed chitinous thickening or

pleurosternal suture; palpus triarticulate, the femur produced at distal internal angle and also with smaller processes at distal external angle.

Coxosternum of prehensorial feet without chitinous lines. Prehensorial feet large, much exposed from above, the articles denticulate within. Basal plate trapeziform, strongly narrowed cephalad.

Ventral pores absent.

Last ventral plate wide. Coxopleural pores small, few.

Anal pores present, distinct.

Anal legs unarmed with claws; with seven joints distad of coxopleura, the ultimate very small.

TYPE. *Watophilus alabamæ*, sp. nov.

#### WATOPHILUS ALABAMÆ, sp. nov.

Body but little attenuated cephalad, very strongly attenuated caudad of middle.

Caudally yellow, the anterior portion more brownish, fulvous; head and prosternum with prehensorial feet darker, light chestnut; antennae pale brownish, lighter distad.

Head longer than wide in ratio 3:2, nearly; of about equal breadth anteriorly and posteriorly or a little narrower caudad; anterior margin with each lateral portion, straight, the two meeting at median line in a very obtuse angle, the anterolateral angles rounded; sides at middle straight and subparallel, a little converging caudad and cephalad; provided with a few scattered bristles subdefinitely arranged (Plate 1, fig. 7). Basal plate trapeziform, about  $\frac{1}{4}$  as long as the cephalic plate, not quite three times wider than long. Prebasal plate not exposed.

Labrum having each lateral piece with but few (mostly about 3 or 4) large spinescent processes from margin; the median piece with about 10 small spines, its free face covered with long seriatly arranged bristles. Lappets of first maxillae very long.

Antennae short, somewhat attenuated; articles compactly disposed, all short; the ultimate about equal in length to the two preceding taken together; very sparsely hirsute, the hairs of distal articles becoming more numerous and smaller; mostly but about  $1\frac{3}{8}$  as long as the cephalic plate.

Prosternum almost exactly equal in length and breadth; anterior mesial margin substraight, but little excised; chitinous lines absent. First joint of prehensorial feet long, rather narrow, its outer length

to the median length of prosternum nearly as 3:5, length to greater width as 3:2; claws strongly curved, when closed extending beyond the front margin of head and nearly attaining end of first antennal article; claw at base with a rather long, apically truncate, subcylindrical tooth; the prefemur with two subdentiform but not strongly chitinized processes, one at distal end and one at proximal end of an excavation (Plate 1, fig. 6).

Dorsum bisulcate as usual, the sulci very fine and also with a fine median sulcus; sparsely hirsute with short straight hairs. Prescuta of middle region moderately long to long, becoming very short cephalad and caudad.

Spiracles all circular, the first much larger than the second, the others decreasing from the second caudad.

First pair of legs distinctly reduced; the posterior pairs clearly more slender than the anterior.

Anterior ventral plates with a median longitudinal sulcus which on the first ones does not extend cephalad of the middle where it ends abruptly but on others reaches cephalic margin and is crossed by transverse depression. Anterior plates with caudal margin extended and fitting into shallow excavation of succeeding one. No ventral pores detected.

Last ventral plate wide; caudal margin straight, the sides converging caudad. Coxopleural pores mostly 4 to 8 of which 2-4 are commonly covered by the ventral plate; when the larger number of pores is present, some may be on lateral portion of coxopleura.

Anal legs much longer and more crassate than penult in both male and female. Without claw, in its place ending in the minute process suggesting an additional article.

Anal pores distinct, moderately large, relatively.

Pairs of legs uniformly 49 in the male, and 51 in the female.

Length of male ad. 14 mm.; of female up to 22 mm.

LOCALITIES.—Anniston and Maplesville, Ala.; Tallulah Falls, Ga.

#### GNATHOMERIUM Ribaut.

Bull. Soc. hist. nat. Toulouse, 1910, p. 106.

#### GNATHOMERIUM UMBRATICUM (McNeill).

*Mecistocephalus umbraticus* McNeill, Proc. U. S. N. M., 1887, 10, p. 332.

*Gnathomerium americanum* Ribaut, Bull. Soc. hist. nat. Toulouse, 1910, p. 120.

LOCALITIES.— Watervalley and Grenada, Miss.; ?Maplesville, Ala.; Bremen, Tallulah Falls, Ga.; Landrum, S. C.; Salisbury, Saluda, Hot Springs, Linville Falls, and Catawba, N. C.; Lynchburg, Balcony Falls, and Natural Bridge, Va.; White Sulphur, W. Va.; Fulton and Lexington, Ky.; Altapass, Unaka Springs, Johnson City, and Russellville, Tenn. (also Knoxville, Beaver Creek, and Mossy Creek, Tenn., seq. Bollman).

Among some specimens secured at Russellville there was a female with very recently hatched young about which her body was still coiled.

### LINOTENIIDAE.

LINOTENIA C. L. Koch.

System der Myriopoden, 1847, p. 86.

The following key will aid in the recognition of the species.

#### Key to species.

- a. Pairs of legs less than 60.
  - b. Pairs of legs of male 47–55; of female 49–59. *L. fulva* (Sager).
  - bb. Pairs of legs 37–45.
    - d. Caudal margin of head angularly extended from sides to median line; basal plate three times as wide as long.
      - L. chionophila* (Wood).
    - dd. Caudal margin of head straight or a little incurved; basal plate but twice or at most 2.5 times as wide as long.
      - L. branneri* Bollman.
  - aa. Pairs of legs in male 67–71; in female 71–81. *L. bidens* (Wood).

#### LINOTENIA FULVA (Sager).

*Strigamia fulva* Sager, Proc. Acad. nat. sci. Phil., 1856, p. 109.

*Strigamia bothriopa* Wood, Journ. Acad. nat. sci. Phil., 1862, ser. 2, 5, p. 46. Trans. Amer. philos. soc., 1865, new ser., 13, p. 182.

*Scolioplanes bothriopus* (Wood) Meinert, Proc. Amer. philos. soc., 1886, 23, p. 222.

*Scolioplanes robustus* Meinert, Proc. Amer. philos. soc., 1886, 23, p. 224.

*Linotenia robusta* (Meinert) Bollman, Entom. Americana, 1888, 4, p. 4. Bull. 46 U. S. N. M., 1893, p. 76.

*Linotenia fulva* (Sager) Bollman, Bull. 46 U. S. N. M., 1893, pp. 92, 98, 109, 184.

LOCALITIES.—Gainsville, Bremen, Lula, and Tallulah Falls (also Indian Springs seq. Bollman), Ga.; Landrum and Taylor's, S. C.; Saluda, N. C.; Russellville, Unaka Springs, and Johnson City (also Mossy Creek and Beaver Creek seq. Bollman), Tenn.; Chatham, Natural Bridge, and near Washington, Va.; White Sulphur, W. Va.; Fulton, Ky.

This, the most common *Linotenia* in the northern states, is also well distributed in the northern part and mountainous sections of the southern states. The southern specimens are larger on the average than northern specimens and show a tendency toward an increased number of legs, males often having as many as 53 and 55 pairs and the females as many as 57 and 59 pairs. At first it seemed that the specimens represented a distinct species; but more careful study of material from many localities shows that intergradation is complete and leaves no satisfactory basis upon which to maintain Meinert's *robusta*, which agrees with these southern specimens. The increased number of legs is a phenomenon met with in various members of this order which have a wide range in proceeding from northern localities to more southern or in going from high altitudes to low. Meinert describes *robusta* as nearly glabrous; but the condition of his type shows this to be due to rubbing. In the antennae of specimens preserved in alcohol there may be considerable variation due in some specimens to differences in the degree of telescoping of the articles, and in some to differences in the recentness of moulting. In the type of *robusta* the articles are well separated so that the shortness of the ultimate article in comparison with the two preceding is exaggerated.

#### LINOTENIA CHIONOPHILA (Wood).

*Strigamia chionophila* Wood, Journ. Acad. nat. sci. Phil., 1862, ser. 2, 5, p. 50. Trans. Amer. philos. soc., 1865, new ser., 13, p. 189.

*Scolioplanes chionophilus* (Wood) Meinert, Proc. Amer. philos. soc., 1886, 23, p. 223.

LOCALITY.—Lexington, Ky.

Ten specimens were secured by the writer at Lexington, Ky., on

August 18, this being the only point for the species thus far recorded within the region covered by the present paper. The species is a boreal one very common in Alaska and neighboring islands and in parts of Canada and is also frequent in the northern sections of the United States. *L. branneri* Bollman seems to replace it in the southern states.

LINOTENIA BRANNERI Bollman.

Ent. Americana, 1888, 4, p. 4.

?*Scolioplanes chionophila* Brölemann, Ann. Soc. ent. France, 1896, 65, p. 60.

Rather robust; very strongly attenuated cephalad, less strongly caudad; body and appendages subdensely clothed with rather long stiff hairs.

In alcohol reddish brown or ferruginous, paler caudad and cephalad; head deeper, paler in front of frontal suture; antennae and legs light brown, uniform.

Head relatively wide anteriorly; anterior margin straight in middle, evenly rounded laterally; caudal margin in middle straight or but little excurved, laterally evenly rounded; widest at about junction of middle and caudal thirds; a marked longitudinal median furrow along entire length of head in caudal portion of which there is a short, sharply impressed sulcus; wider than long in about ratio 6:5. Basal plate a little overlapping the caudal margin of the cephalic; a little wider than the head, and very nearly twice as wide as long or a little more.

Antennae moderately long, the articles long or moderately long, gradually decreasing in length from the fifth or sixth to the penult; ultimate article almost exactly equalling in length the two preceding taken together; usually four times, a little more or less, than the head, in the specimen described ad 2.5 mm.

Claws of prehensorial feet when closed attaining the front margin of the head but not at all extending beyond; tooth of claw stout, conical, extending mesocephalad; femora wider than greatest length nearly in ratio 3:2, twice as long as the outer height of the prefemur; caudal margin straight, not at all produced caudad in middle.

Anterior prescuta moderate, about  $\frac{1}{2}$  as long as the main scutum of segment, very gradually increasing caudad to the third fourth of length where they are about  $\frac{1}{2}$  as long as main scuta, and then again decreasing caudad. Dorsum with a longitudinal median furrow which may be obscure in some parts.



Spiracles all circular and of very nearly the same diameter throughout length of body.

First legs but little reduced, the second of normal size.

Ventral pores in a broad band along caudal border of each anterior plate, the band on more caudal segments dividing into two areas as usual.

Last ventral plate narrow, sides converging caudad; posterior end of plate extended caudad and narrowly rounded. Coxopleurae of segment bearing about 16 pores, large and small, on ventral surface.

Anal legs in female ending in a large claw; about equalling the penult legs in length and thickness. Anal legs in male strongly crassate, thickest at middle of length; subdensely clothed with finer, and moderately long hairs.

Anal pores rather large, usually concealed from ventral side.

Pairs of legs in female 41-43; in males uniformly 41.

Length of female 27 mm.; width ad 1.2 mm. Length of male 22 mm.

LOCALITIES.—Tallulah Falls and Bremen, Ga.; Taylor's, S. C.; Russellville, Tenn.; Brown's Summit, N. C.; Natural Bridge, Va. The type, a female, is from Arkansas.

The female upon which the above description is almost wholly taken is from Tallulah Falls.

var. *MIURA*, var. nov. Agreeing with typical form excepting in its apparently smaller size, which seems to approximate that of *chionophila*, and especially in the greater shortness of the antennae which likewise are very much in proportion and appearance like those of *chionophila*. The antennae are mostly but three times, a little more or less, as long as the head whereas in the typical form, as above indicated, they are from nearly four to somewhat more than four times as long. While some specimens seem to indicate intergrading, in my material there are evidently two modes of length in the antennae. It seems better, therefore, for the present at least to indicate the two forms.

LOCALITIES.—Fulton, Ky.; Gainesville, Ga.; Saluda, N. C.; Altapass and Russellville, Tenn.

#### LINOTENIA BIDENS (Wood).

*Strigamia bidens* Wood, Journ. Acad. nat. sci. Phil., 1862, ser. 2, 5, p. 47. Trans. Amer. philos. soc., 1865, new ser., 13, p. 183.

*Scolioplanes ruber* Bollman, Amer. nat., 1887, 21, p. 82. Ann. N. Y. acad. sci., 1888, 4, p. 110. Bull. 46, U. S. N. M., 1893, p. 132.

*Scolioplanes bidens* (Wood), Brölemann, Ann. Soc. ent. France, 1896, 65, p. 58, pl. 6, fig. 10-13.

Color in alcohol light brown, the sides and venter paler; head with prosternum and prehensors dark reddish, the frontal region paler; antennae reddish brown, pale distad. In life the color is bright red.

Head widest at caudal end, strongly narrowed from about the caudal fourth cephalad, the sides of the caudal fourth subparallel; caudal margin slightly excurved anterior margin nearly straight between antennae, oblique laterally; a median longitudinal sulcus on caudal portion; wider than long in about ratio 9:8. Frontal plate not discrete. Prebasal plate not exposed. Basal plate 3.5 times wider than long.

Antennae filiform, not at all attenuated distad; ultimate article clearly shorter than the two preceding taken together; of medium length, in specimen described 2 mm.

Prosternum about 2.3 times wider than median length, 3 times wider than lateral length, the length at side about equalling the outer length of prefemur.

Anterior prescuta moderately short, about  $\frac{1}{3}$  as long as main plate, increasing in length caudad and in the posterior region becoming  $\frac{1}{2}$ , or a little more, the length of main scutum.

Spiracles large, circular, the first larger than the second in the ratio 5:4, others only very gradually decreasing in size toward the caudal end of the body, those at caudal end smaller than the second and immediately succeeding ones in ratio 4:3.

First legs reduced, the succeeding several pairs gradually increasing to full size; legs almost glabrous proximally, bearing but scattered and very short hairs, these more abundant on distal joints.

Ventral pores in a moderately wide transverse band along caudal border, this band scarcely indicated on first few sterna, but on most clearly separated into two adjacent areas. Each sternum with a cruciform impression, the longitudinal sulcus being the more deeply impressed and widening at middle of length into a shallow pit; the transverse sulcus often broken into a number of parallel impressions or lines and becoming more deeply impressed on caudal segments.

Last ventral plate narrow, conspicuously narrowed caudad where it runs to an angle; sides nearly straight (Plate 2, fig. 2). Coxopleurae much enlarged, bearing on ventral surface numerous (ad 24) small pores.

Anal pores present, small.

Anal legs in male strongly crassate; densely clothed with fine, short and straight hairs; ending in a small short claw (Plate 2, fig. 2).

Pairs of legs (male) 67.

Length 41 mm.; greatest width 1.4 mm.; length antennae 2 mm.

LOCALITIES.—Watervalley, Miss.; Lula, Bremen, and Tallulah Falls, Ga.; Raleigh, Saluda, Linville Falls, and Brown's Summit, N. C.; Altapass, Russellville, and Johnson City (also reported as *L. ruber* from Mossy Creek, and Beaver Creek by Bollman), Tenn.; Lynchburg, Va.; Lexington, Ky.

The description above is of a male from Lexington.

I am unable to find grounds for regarding the specimens here listed as *bidens* as constituting more than one species, although there is considerable variation in some features. By far the majority of females have 71 or 73 pairs of legs; but others have 75, 77, 79 and one has 81 pairs of legs and all without showing any structural differences of importance. The males have mostly either 67 or 69 pairs of legs.

#### AGATHOTHUS Bollman.

Bull. 46, U. S. N. M., 1893, p. 166.

Frontal plate present. Basal plate wide. Prebasal plate in type species absent. Antennae filiform. Dorsal plates not bisulcate.

Labrum free; tripartite, with the middle piece very large, bowed outward, and fringed with spines along its free margin; lateral pieces with margin smooth or weakly crenate, not armed, overlapped at mesial ends by the middle piece.

Outer process of first maxillae biarticulate, without lappets, apical joint somewhat membranous distad; inner process not separated, coxae not separated by median suture. Coxae of second maxillae completely fused; palpus ending in a small, simple claw.

Prosternum without chitinous lines; anteriorly medianly emarginate. Claw of prehensors wholly unarmed, constricted at base and excavated above, being thin dorso-ventrally at proximal end (Plate 2, fig. 11).

Ventral pores in a transverse band in front of caudal margin.

Last ventral plate very wide. Coxopleurae with a number of moderately large pores.

Anal pores in type species concealed.

Anal legs composed of six joints, terminating in a claw.

**TYPE.** *Agathothus gracilis* Bollman.

This genus, the affinities of which have been heretofore wholly problematical, is very close to *Linotenia* as is evident from the diagnosis above. It seems proper to group these two genera in a distinct subfamily, *Linoteniinae*, as indicated in the key (p. 410). But one species is known.

**AGATHOTHUS GRACILIS (Bollman).**

*Scolioplanes gracilis* Bollman, Ann. N. Y. acad. sci., 1888, 4, p. 110.

*Agathothus gracilis* (Bollman) Bollman, Bull. 46, U. S. N. M., 1893, p. 166.

Very gradually attenuated cephalad, more abruptly caudad; sparsely hirsute with short straight hairs.

Yellow; the head with prosternum and prehensorial feet darker, brownish; antennae and legs light yellow.

Head wider than long in ratio 2.2:2; subquadrate; the anterior margin mesally truncate, laterally a little oblique; lateral margin nearly straight over middle part of length, curving mesad at ends; caudal margin very slightly overlapped by the basal plate. Frontal plate discrete. Basal plate nearly  $2\frac{1}{2}$  times as wide as long at middle, a little wider than the cephalic plate.

Antennae filiform, the first article wider than others; joints all short excepting the ultimate which is much longer than the two preceding taken together, articles gradually decreasing in length from the second to the penult inclusive; about 3.25 times as long as head; clothed with short hairs which on proximal articles are sparse but become denser distad.

Claws of prehensorial feet very long, when closed nearly attaining the front margin of head, widest above base where they are constricted and also excavated dorsally so as to be thin dorsoventrally and blade-like; all articles lacking denticles; very sparsely hirsute. Anterior median margin of prosternum moderately deeply sinuate; prosternum glabrous or nearly so except laterally; wider than long in ratio 23:13.

Anterior prescuta very short, gradually increasing in length, caudad, becoming moderate or long in middle and posterior regions, where they do not differ much in length.

Spiracles all circular, the first larger than the second, the second and third equal and the ultimate ones but little smaller.

Legs of the first pair but little reduced; anterior and posterior pairs subequal in length and thickness; rather sparsely hirsute.

Ventral pores in a transverse band along caudal border; ventral plates with a median longitudinal sulcus.

Last ventral plate, very wide, cephalic and caudal margins straight, the lateral weakly excurved and strongly converging caudad. Coxopleurae inflated; with a few pores of moderate size or large arranged close to edge of ventral plate and partly covered by it, in the specimen being described in one series, but sometimes in two.

Anal pores present, of moderate size, covered from ventral view.

Anal legs ending in a long claw; in the female proportionately rather slender, but decidedly thicker and longer than the penultimate pair. Anal legs of male strongly and clavately crassate, its ultimate article abruptly conical, short; densely clothed with fine hairs.

Pairs of legs in female 81; in male 77.

LOCALITIES.—Johnson City (and also Beaver Creek and Mossy Creek seq. Bollman), Tenn.

The description above is chiefly that of a partly grown female. Several other specimens were subsequently found in the collection.

#### **SOGONIDAE**, fam. nov.

The two genera for which the present family is established possess in common the following more important characteristics:—

Antennae flattened, conspicuously attenuated distad. Head small or medium in size, leaving the prehensorial feet partly exposed from above.

Mandible without dentate lamellae; with a single pectinate lamella.

Labrum of a single piece apparently, free laterally but fused in middle; free margin as a whole concave, the mesial portion a little convex, fringed with a row of long spines or teeth.

First maxillae with coxae completely fused; inner and outer branches set off by a suture, the outer biarticulate and with membranous lappets.

Second maxillae with coxae completely fused; palpus ending in a simple claw.

Chitinous lines of prosternum strongly developed.

Ventral pores in a narrow transverse band a little caudad of middle of anterior sterna.

Suprascutella absent.

Anal legs five or six jointed; lacking claws.

The two genera as at present known may readily be separated as follows:

Anal legs with five joints distad of coxopleura (a single porigerous pit on each coxopleura.) *Timpina*, gen. nov.

Anal legs with six joints distad of coxopleura; two porigerous pits on each coxopleura. *Sogona*, gen. nov.

SOGONA, gen. nov.

Head rather small. Frontal plate not discrete. Prebasal plate (in type) present. Basal plate wide. Antennae flattened, broad at base and conspicuously attenuated distad. Dorsal plates bisulcate.

Mesial portion of labrum with free margin a little convex, bearing a fringe of long teeth.

Both branches of first maxillae distinctly separated, the biarticulate outer one bearing membranous lappets, in dorsolateral position.

Claw of palps of second maxillae large, simple; sterna completely fused.

Prehensorial feet rather large, partly exposed from above; chitinous lines strongly developed.

Ventral pores in a narrow transverse band immediately behind middle of anterior ventral plates.

Last ventral plate wide. Coxopleural pores opening into two large pits on each side, which are covered by the ventral plate.

Anal legs with six joints, clawless.

TYPE.—*Sogona minima*, sp. nov.

SOGONA MINIMA, sp. nov.

Slender, attenuated cephalad and caudad; body with scattered short hairs, those on legs more numerous but still sparse.

Yellow: head with prosternum and prehensorial feet reddish brown.

Anterior margin of head with lateral margins straight and somewhat oblique, meeting at mesial line in an obtuse angle; sides of head weakly excurved from end to end. Head with but few scattered hairs. Almost exactly equal in length and breadth or a trifle longer than wide; three times as wide as the median length of basal plate. Prebasal plate exposed. Basal plate more than three times wider than the median length.

Antennae moderate or short, the articles decreasing in length distad to the penult; flattened or compressed, attenuated from base distad; ultimate article longer than the two preceding taken together

(ad 7: 6); sparsely hirsute at base, the hairs becoming finer and shorter and more dense distad.

Claws of the prehensorial feet when closed not fully attaining the front margin of head; all joints unarmed; prosternum wider than long in the ratio 11:8; chitinous lines distinctly developed; marked with a distinct median sulcus; anterior median margin only a little angularly depressed mesially; almost glabrous, bearing but a few scattered hairs.

Anterior prescuta very short, others short.

Spiracles round or the first few weakly obliquely subelliptical; the first one clearly larger than the second; first or anterior ones large, decreasing caudad, the posterior ones becoming small.

Each ventral plate with a deep longitudinal median sulcus; anterior sterna angularly extended caudad at middle in a process which fits into a corresponding pit in the succeeding plate. Ventral pores present on anterior plates; few in number and arranged in a narrow transverse band extending across plate between middle and caudal margin, the band widest at median line and running out to a point on each side.

Last ventral plate very wide; sides converging caudad, appearing a little convex; caudal margin straight; sparsely hirsute. Coxopleurae with two large pits on each side, these covered beneath edge of ventral plate.

Anal legs without a claw. In the female thicker and much longer than the penult; sparsely hirsute with long hairs excepting for limited areas on ventral surfaces of joints which are densely clothed with patches of shorter hairs (Plate 3, fig. 2). Anal legs in male strongly crassate.

Anal pores small, concealed in ventral view.

Pairs of legs in female 53-55; in male 51.

Length of female 16 mm.; of male 12.5 mm.

LOCALITIES.—Taylor's, S. C.; Johnson City, Tenn.

At Johnson City a female, described above, was taken with her young, about which her body was coiled.

#### TIMPINA, gen. nov.

Prebasal plate in type absent; frontal suture absent. Basal plate wide. Antennae of moderate length; conspicuously flattened; attenuated from base distad; dorsal plates bisulcate.

Labrum apparently of one piece which is free laterally and fused mesially as in the preceding genus; free margin at middle a little convex, fringed with long teeth.

Mandibles with a single pectinate lamella; no dentate lamella.

First maxillae with sterna completely fused; inner and outer branches distinctly set off by suture; the outer biarticulate, with long lappets.

Sterna of second maxillae also completely fused as indicated in description of family; palpus with a simple claw of normal size.

Prehensorial feet conspicuously exposed from above; all articles devoid of teeth; chitinous lines strongly developed.

Ventral pores on anterior sterna, few; in a transverse narrow band caudad of middle of plate.

Last ventral plate very wide. Coxopleurae with a single porigerous pit on each side, this partly covered by ventral plate in type.

Anal legs with but five joints beyond coxopleura; clawless.

TYPE.—*Timpina texana*, sp. nov.

#### TIMPINA TEXANA, sp. nov.

Conspicuously attenuated caudad and cephalad.

In the type specimen, bleached in the preservative, the body in general appears yellow at ends and darker, more brown, over middle portions; an obscure geminate dark band along part of dorsum.

Head truncate anteriorly and posteriorly, or the anterior margin slightly convex; anterior and posterior margins subequal; sides over middle portion of length nearly straight or a little excurved, at ends bend in mesad; nearly equal in length and breadth or a little longer than wide (39:38);  $3\frac{1}{4}$  times longer than the basal plate. Prebasal plate not exposed. Basal plate  $3\frac{1}{2}$  times wider than the median length.

Claws of prehensorial feet, which are very short and but little curved, when closed end to end almost exactly even with anterior margin of head; all articles of feet devoid of denticles. Prosternum with anterior median margin weakly incurved; chitinous lines strongly developed; much wider than long (ad 10:7);  $2\frac{1}{2}$  times longer than the prefemur.

Antennae conspicuously flattened and attenuated distad; moderate or short; articles decreasing in length distad to penult; ultimate article of same length as the two preceding taken together or nearly so; proximally clothed with long stiff bristles which distad are re-



placed by shorter and more densely arranged hairs. Length in type 2+ mm.

Prescutellum relatively very large, several times larger than the spiraculiferous plate, which, in turn, is larger than the postscutellum.

The first and second spiracles vertically elliptical, others round or nearly so; anterior ones large, the first larger than the second, others decreasing in size gradually from the second caudad, the posterior ones very small.

Ventral pores apparently present on only about twelve anterior sterna; few in number and arranged in a narrow transverse band a little caudad of the middle of plate, band tapering to ends, extending across plate entirely on first plates, shorter on more caudal ones.

Last ventral plate very wide, anterior and caudal margins straight; lateral margins convex, converging caudad. Coxopleurae moderate, apparently with a single large porigerous pit on each, covered by edge of ventral plate excepting at ectal edge at which the plate is excised to give free passage from pit.

Anal pores obsolete, being closed or nearly so.

Genital palpi in male short, conical, broad at base.

Anal legs much longer than penult, strongly and uniformly crassate. the fifth or ultimate article clawless, not reduced in diameter.

Length 49 mm.; width 1.4 mm.

LOCALITY.—Austin, Texas. One male collected by Prof. T. H. Montgomery.

While this form has not been found strictly within our limits, it may range into the southern portion, and is discussed here because of its interesting relationship to *Sogona*.

## HIMANTARIIDAE.

### GOSIPHILUS Chamberlin.

#### GOSIPHILUS LATICEPS (Wood).

*Strigamia laticeps* Wood, Journ. Acad. nat. sci. Phil., 1862, ser. 2, 5, p. 49. Trans. Amer. philos. soc., 1865, new ser., 13, p. 186.

*Haplophilus laticeps* (Wood), Chamberlin, Ann. Ent. soc. America, 1909, 2, p. 177.

LOCALITIES.—California, Nevada, Texas.

Described originally from Texas. While not actually known from within the district covered by the present paper, its wide distribution across the southern portion of the United States from Texas westward, makes it seem quite likely that it may occur occasionally farther east.

*HAPLOPHILUS* Verhoeff.

*HAPLOPHILUS* GRENADAE, sp. nov.

Slender, gradually attenuated cephalad, the caudal portion more abruptly narrowed; entire body and legs clothed sparsely with short straight hairs.

Light brownish yellow, the caudal portion darker, smoky. Head and prehensorial feet with prosternum pale reddish brown; antennae yellow, darkened distad. Cephalic plate much wider than long (a little more than 4:3); sparsely clothed with short straight hairs; rounded, subcircular, excepting the caudal margin which is substraight and overlaps the basal plate. Free portion of basal plate  $3\frac{1}{2}$  times as wide as long, the head not fully 2.5 times as long as its median length.

Antennae short, not fully contiguous at base, flattened dorso-ventrally and attenuated distad as usual; all articles except the ultimate short, the latter much longer than the two preceding taken together.

Claws of prehensorial feet when closed not attaining front margin of head by a large space; almost glabrous; all joints unarmed; claw stout, moderately curved. Prosternum also almost glabrous; more than twice as wide as long (nearly 2.3:1), not fully twice as long as the prefemur (20:11); anterior margin but weakly sinuate.

Dorsal scuta very obscurely bisulcate. Anterior prescuta short, becoming of moderate length in middle and posterior portions.

Spiracles round, the first not enlarged, all being rather small, and only very gradually reduced caudad.

Ventral plates widely, weakly depressed transversely in line with legs; on posterior of slope of the depression, or partly caudad of it, the ventral pores are arranged in an oblong area which on most plates, especially the more caudal ones, shows a tendency to expand at the ends (Plate 3, fig. 12).

First pair of legs clearly shorter and more slender than the second; posterior pairs clearly longer and more slender than the anterior pairs.

Last ventral plate with sides strongly converging caudad, substraight or a little incurved, caudal margin straight (Plate 3, fig. 11). Coxo-

pleurae of last legs inflated, or bearing numerous pores which are closely arranged over ventral surface and in an irregular series along dorsal plate, the dorsolateral surface being free from pores.

Anal legs in female clearly longer than the penult, not crassate (Plate 3, fig. 11.)

Pairs of legs in the female 67.

Length 26 mm.; greatest width not fully .75 mm.

LOCALITY.—Grenada, Miss.

The type, a single female, was taken July 15.



PLATE 1.

*ARENOPHILUS WATSINGUS*, gen. et sp. nov. Chatham, Va.

- Fig. 1. Ventral view of anterior portion.
- Fig. 2. Ventral view of posterior portion.
- Fig. 3. Dorsal view of anterior portion.
- Fig. 4. Labrum.

*WATOPHILUS ALABAMAE*, gen. et sp. nov. Anniston, Alabama.

- Fig. 5. Ventral view of anterior portion.
- Fig. 6. Ventral view of posterior portion.
- Fig. 7. Dorsal view of anterior portion.

*LINOTENIA FULVA* (Sager). Gainesville, Ga.

- Fig. 8. Ventral view of posterior portion.
- Fig. 9. Ventral view of anterior portion.
- Fig. 10. Dorsal view of anterior portion.

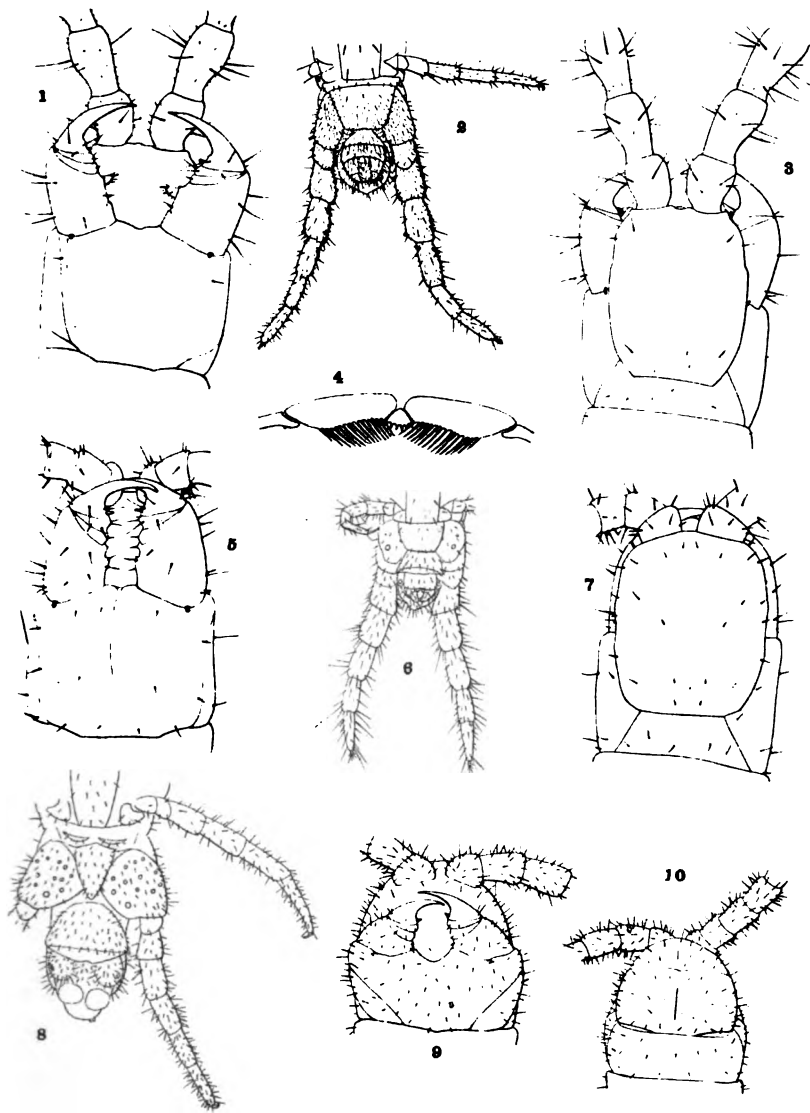








PLATE 2.

LINOTENIA BIDENS (Wood). Lexington, Ky.

- Fig. 1. Dorsal view of anterior portion.
- Fig. 2. Ventral view of posterior portion.
- Fig. 3. Ventral view of anterior portion.

LINOTENIA BRANNERI Bollman. Tallulah Falls, Ga.

- Fig. 4. Ventral view of anterior portion.
- Fig. 5. Dorsal view of anterior portion.
- Fig. 6. Ventral view of posterior portion.

AGATHOTHUS GRACILIS Bollman. Johnson City, Tenn.

- Fig. 7. First and second maxillae, one side.
- Fig. 8. Labrum.
- Fig. 9. Ventral view of posterior portion.
- Fig. 10. Dorsal view of anterior portion.
- Fig. 11. One prehensor with part of prosternum.

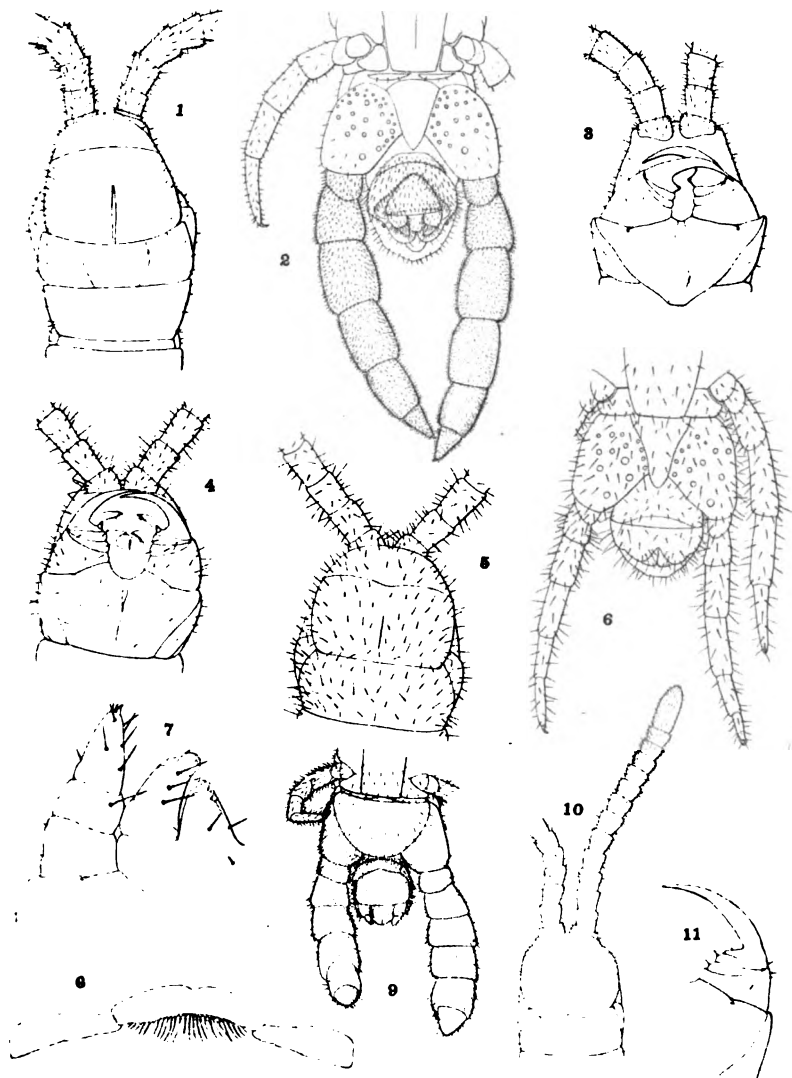






PLATE 3.

*SOGONA MINIMA*, gen. et sp. nov. Johnson City, Tenn.

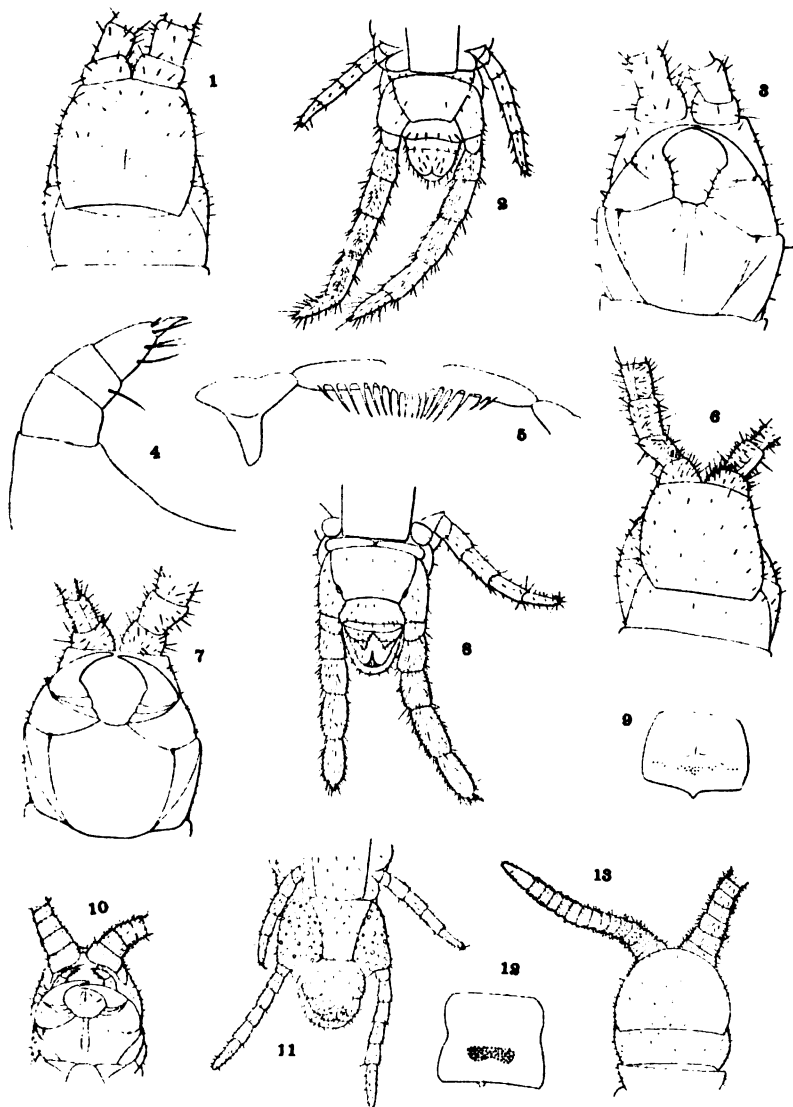
- Fig. 1. Dorsal view of anterior portion.
- Fig. 2. Ventral view of posterior portion.
- Fig. 3. Ventral view of anterior portion.
- Fig. 4. Palpus of second maxilla.
- Fig. 5. Labrum.
- Fig. 9. An anterior ventral plate, showing pores.

*TIMPINA TEXANA*, gen. et sp. nov. Austin, Texas.

- Fig. 6. Dorsal view of anterior portion.
- Fig. 7. Ventral view of anterior portion.
- Fig. 8. Ventral view of posterior portion.

*HAPLOPHILUS GRENADAÆ*, sp. nov. Grenada, Miss.

- Fig. 10. Ventral view of anterior portion.
- Fig. 11. Ventral view of posterior portion.
- Fig. 12. Tenth ventral plate, showing pores.
- Fig. 13. Dorsal view of anterior portion.











# NEW NORTH AMERICAN CHILOPODS AND DIPLOPODS.

By RALPH V. CHAMBERLIN,  
University of Pennsylvania, Philadelphia.

## CLASS CHILOPODA.

Family LITHOBIIDÆ.

Genus *Arenobius* Chamberlin.

*Arenobius coloradanus* sp. nov.

Dorsum from testaceous to dark brown and dull chestnut with the posterior plates and the first one usually not all darkened. Head mostly the same color as dorsum or very nearly so, or somewhat more reddish. Antennæ concolorous with head, pale distad. Venter from yellow or testaceous to dark brown, the caudal plates usually a little darker. Prosternum and prehensorial feet of same color as head or nearly so. Legs of same color as adjacent portion of venter.

Head widest at level of marginal interruptions; clearly wider than long (11: 10); caudal margin straight. Depressed or furrowed parallel with frontal suture a little cephalad of the latter, from this furrow a median longitudinal furrow extending toward anterior margin. Two, usually clearly impressed, longitudinal furrows on caudal region of head, one a little each side of the middle and the two united in front of the posterior margin by a transverse furrow. Smooth and shining.

Dorsal plates all very finely or obscurely roughened, appearing smooth and shining to the naked eye; usually no furrows distinctly developed excepting the usual depression or furrow immediately within the caudal and lateral margins and on some the short transverse mark on each side near margin at about one-third length of plate from caudal margin. Posterior angles of ninth, eleventh and thirteenth dorsal plates strongly produced; posterior angles of other minor plates rounded or obliquely excised.

Ventral plates all punctate and finely roughened; impressed with three longitudinal furrows of which the median is most distinct, the latter on some of the more posterior plates ending caudad in a deeper pit or depression about one-third the length of plate from caudal edge; mostly with a rather wide transverse depression or furrow caudad of middle of plate. Sometimes an additional longitudinal furrow showing on each side between the median and the lateral, the caudal end often curving mesad to unite with its mate at middle; this furrow often more or less united with the lateral one. The last several plates sometimes with furrows very obscure or practically absent.

Antennæ short or very short, reaching the sixth or seventh segment; articles 30 to 35, the second very long with those more distad much shorter, cylindric, subuniform or, more usually, with longer articles occurring singly at intervals among the shorter ones, in general decreasing in size distad. Hairs of medium length.

Eyes composed mostly of from 9 to 12 ocelli arranged in three series; e. g., 1 + 3, 3, 2, 1 + 4, 3, 3, 1 + 4, 4, 3,. The single ocellus much largest, subvertically elliptic or oval.

Prosternum about 1.6 times wider than long. Teeth 2+2, small acute. Median incision wide and moderately deep, its sides concave. Spine on each side well ectad of outer tooth, much more slender than teeth but stouter at base than neighboring hairs, bristle like distad.

Coxal pores circular, well separated; in number arranged as follows: 3, 4, 4, 3; 3, 4, 4, 4; 4, 5, 5, 5.

Coxæ of anal legs armed laterally and dorsally; other coxæ seemingly unarmed. Spines of first legs  $\frac{0, 0, 2, 1, 1}{0, 0, 1, 2, 1}$  or  $\frac{0, 0, 2, 1, 1}{0, 0, 1, 3, 1}$ ; of the second and third  $\frac{0, 0, 2, 2, 1}{0, 0, 2, 3, 1}$ ; of the fourth  $\frac{0, 0, 3, 2, 2}{0, 0, 2, 3, 1}$  or, occasionally,  $\frac{0, 0, 3, 2, 1}{0, 0, 2, 3, 1}$ ; of the fifth  $\frac{0, 0, 3, 2, 2}{0, 0, 2, 3, 1}$ ; of the sixth to the eleventh,  $\frac{0, 0, 3, 2, 2}{0, 0, 2, 3, 2}$ ; of the twelfth and thirteenth,  $\frac{0, 0, 3, 2, 2}{0, 0, 3, 3, 2}$ ; of the penult,  $\frac{0, 0, 3, 2, 2}{0, 1, 3, 3, 2}$  in the female, or  $\frac{0, 0, 3, 2, 1}{0, 1, 3, 3, 2}$  in the adult male, each having claw armed with two accessory claws; of anal,  $\frac{1, 0, 3, 2, 1}{0, 1, 3, 3, 1}$ , the dorsal spine of tibia and also outer one of femur readily lost so that spining may appear thus,  $\frac{1, 0, 3, 2(1) 0}{0, 1, 3, 3, 1}$ , two accessory claws present as in the penult pair. In the female the anal legs are short and very slender, decreasing gradually in diameter from the femur distad, the tibia being intermediate in diameter between femur and first tarsal article as the latter is between tibia and second tarsal article; tibia rather weakly longitudinally furrowed along dorsal surface. Penult legs similar to anal except for smaller size. In the male the anal legs are also rather slender but the tibia is crassate, being fully as thick as the femur and being widest at distal end and abruptly thicker than the first tarsal joint, its dorsal surface shallowly depressed, a longitudinal dorsal furrow also present on femur and prefemur, that of the latter less distinct. Penult legs of male also slender, with joints dorsally longitudinally furrowed; the tibia obliquely excised at dorso-caudal corner of distal end and bearing at this place a small, flattened lobe or crest which is transverse to the axis of the joint, this lobe bearing a few short hairs but nothing like the brush in manegitus.

Gonopods of male relatively wide, flattened, truncate distad; bearing mostly 4-6 bristles in a transverse row along distal edge of ventral side.

Gonopods of female with claw entire, long and stout, acutely pointed, considerably curved, darkened distad. Basal spines 2 + 2, subequal or with the inner in some individuals considerably shorter, stout; in ventral view acutely conical in outline. Articles, especially the second and third, glabrous or nearly so on ventral and mesal surfaces, but clothed with a moderate number of bristles on ectal and dorsal surfaces.

Body rather slender being about 7.5 times as long as width of tenth plate; conspicuously attenuated cephalad from eighth plate, with the first plate much narrower than the third. Width of head, first, third, eighth and tenth dorsal plates to each other as 40, 33, 37, 47 and 47, the eighth and tenth plates being equal and manifestly considerably wider than the head.

Length from 12 to 15 mm. A male 13 mm. has antennæ 5 mm. long and anal legs exclusive of coxa, circa 4.8 or 5 mm. long, with the tenth plate about 1.7 mm. wide.

Locality: Manitou, Colorado (author, Aug., 1910).

***Arenobius sontus* sp. nov.**

Brown to deep mahogany. Head in some degree darker than dorsum. Antennæ chestnut, paler distad. Prosternum brown to mahogany, paler than head. Venter testaceous to deep brown, the caudal plates darkest. Legs testaceous to brown, the posterior pairs darker with their tarsi usually paler.

Head and first dorsal plate smooth and shining; other dorsal plates rugose, the more caudal ones more strongly roughened than the anterior ones.

Antennæ of moderate length, reaching the seventh segment. Composed of from 40 to 50 articles which beyond the first ones become short, often showing an alternation of a very short article with longer ones in groups between.

Eyes composed of mostly 9 to 12 ocelli arranged in three series; thus, 1+3, 4, 2.

Prosternal teeth 2+2, the two fused at base in a dental plate, the inner larger than the outer and both much stouter than the ectal spines which, nevertheless, is stout and tooth-like and not at all bristle-tipped.

Coxal pores circular decreasing markedly in size proximad, the most distal being large; in number and arrangement, 5, 5, 5, 4; 5, 5, 5, 5; 6, 6, 6, 5, etc. None of the posterior coxæ armed laterally. Spines of first legs,  $\frac{0, 0, 2, 1, 1}{0, 0, 1, 3, 2}$  or  $\frac{0, 0, 2, 1, 1}{0, 0, 1, 2, 2}$ ; of second  $\frac{0, 0, 2, 2, 1}{0, 0, 2, 3, 2}$ ; of third to sixth,  $\frac{0, 0, 2, 2, 2}{0, 0, 2, 3, 2}$ ; of seventh and eighth,  $\frac{0, 0, 3, 2, 2}{0, 0, 2, 3, 2}$ ; of ninth and tenth,  $\frac{0, 0, 3, 2, 2}{0, 0, 3, 2, 2}$ ; of eleventh,  $\frac{1, 0, 3, 2, 2}{0, 0, 3, 3, 2}$ ; of twelfth,  $\frac{1, 0, 3, 2, 2}{0, 1, 3, 3, 2}$ ; of penult,  $\frac{1(2), 0, 3, 2, 2}{0, 1, 3, 3, 2}$ ; of anal,  $\frac{1(2), 0, 3, 2, 1}{0, 1, 3, 2, 1}$ , with two claws, the penult having three. As noted in the formulæ, the dorsal spine of the posterior coxæ is frequently replaced by two situated close together. The anal legs of the male slender, the tarsal joints especially slender; tibia bearing near distal end of its mesal surface toward dorsal side a small, flattened, subtriangular lobe or crest the long axis of which is parallel to that of the joint and its higher end caudad, its mesal or long edge somewhat convexly curving. Penult legs slender bearing no special lobes. Gonopods of male rather large and broad, conspicuously exposed; distally rounded, bearing about ten or twelve long bristles.

Gonopods of female with claws very long and stout, moderately curved. First article excavated on mesal side toward base as usual, this side strongly chitinized as usual. Basal spines 2+2, large and stout, well separated, the outer larger than the inner on each side.

Gradually and considerably attenuated cephalad, the first plate narrowest as usual.

Length from 22 to 30 mm. A male 26 mm. long has antennæ 11 mm. long and anal legs as 9.5 mm. long with its tenth plate as 3.1 mm. wide.

Locality: Mexico (Guadalajara and Tuxpan).

Genus **Guambius** gen. nov.

*Type*.—*Lithobius euthus* Chamberlin.

Other known species belonging to this genus are *pinguis* Bollman, *curtior* Chamberlin and *mississippiensis* sp. n. described below.

**Guambius mississippiensis** sp. nov.

Dorsum dilute chestnut, with the caudal plates and a median longitudinal line somewhat darker. Head and antennæ dark chestnut, the latter paler distad. Venter testaceous, darker brown caudad. Prosternum and prehensorial feet nearly the same as head. Legs testaceous, the caudal pairs a little darker.

Head slightly wider than long (36: 35 or 34.5); widest at marginal interruptions, between which and the eyes the diameter is nearly uniform, the sides caudad of this convex and strongly converging; the median portion of caudal margin straight. Rather strongly transversely furrowed or depressed immediately in front of caudal marginal thickening, the furrow extending entirely across head and continuous with caudal ends of a wide longitudinal furrow extending cephalad dorsal of level of eyes on each side. A short transverse sulcus a little cephalad of and parallel with median part of frontal suture, a median longitudinal sulcus extending forward from this transverse one and showing or passing through a deeper pit-like impression at middle of length. Smooth and shining, or only very obscurely uneven.

Dorsal plates finely roughened. Major plates, excepting the seventh, showing distinctly the short transverse submarginal sulcus on each side about beginning of caudal third of plate, the seventh plate showing a similar sulcus near each caudal corner and one near each anterior corner as well. Most of the major plates marked with two distinct longitudinal sulci which diverge more or less from near the caudal margin cephalad, these sulci in some distinct only cephalad of the submarginal transverse marks. Posterior angles of eleventh and thirteenth plates a little produced, those of others rounded or obliquely excised.

Most ventral plates with a rather deep longitudinal furrow toward each side but mesad of a weaker submarginal furrow also present. The usual median longitudinal furrow with also the transverse depression cephalad of caudal margin also more or less evident.

Antennæ very short, reaching to or nearly to the sixth segment; articles 25, of which the second is longest, those immediately following not abruptly shorter but only very gradually decreasing in size distad.

Eyes about 11 to 14 in number, arranged in four series; thus, 1+5, 4, 3, 1 and 1+4, 3, 2, 1. The single ocellus much the largest, sub-vertically elliptic or oval.

Prosternum 1.5 times wider than long or slightly more. Teeth 2+2, subequal, acute, with line of apices manifestly recurved. Median incision rather wide and deep with its sides concave. Ectal spines much more slender than the teeth, bristle-like distad, acute.

Coxal pores circular, of moderate size; in number, in type specimen, 3, 4, 4, 3.

No spines of posterior coxæ evident. Spines of first legs  $\frac{0, 0, 1, 1, 1}{0, 0, 1, 2, 1}$ ; of second,  $\frac{0, 0, 1, 2, 1}{0, 0, 1, 2, 1}$ ; of third,  $\frac{0, 0, 1, 2, 1}{0, 0, 1, 2, 1}$  or  $\frac{0, 0, 1, 2, 2}{0, 0, 1, 3, 1}$ ; of fifth and sixth,  $\frac{0, 0, 1, 2, 2}{0, 0, 1, 2, 2}$ ; of seventh,  $\frac{0, 0, 1, 2, 2}{0, 0, 2, 2, 2}$ ; eighth to tenth,  $\frac{0, 0, 2, 2, 2}{0, 0, 2, 2, 2}$ ; eleventh,  $\frac{0, 0, 2, 2, 2}{0, 0, 2, 2, 2}$  or  $\frac{0, 0, 2, 2, 2}{0, 0, 2, 3, 2}$ ; of twelfth,  $\frac{0, 0, 3, 2, 2}{0, 0, 2, 2, 2}$ ; of thirteenth,  $\frac{0, 0, 3, 2, 2}{0, 1, 2, 3, 2}$ ; of the penult,  $\frac{0, 0, 3, 1(2), 0(1)}{0, 1, 3, 3, 1}$ , armed with two claws; of the anal  $\frac{0, 0, 3, 2, 1}{0, 1, 3, 3, 1}$ , claws in type broken off. The anal legs of male strongly crassate, the prefemur particularly elevated dorsally; femur conspicuously excavated dorsally, the excavation extending from end to end as a broad and rather deep furrow; the tibia much less swollen than the femur, complanate or shallowly furrowed longitudinally on dorsal surface; hairs short and straight, more numerous on dorsal surface of all joint but nowhere dense or forming bunches; articles not laterally furrowed. Penult legs crassate in about same degree as the anal but the tibia relatively larger; distal end of tibia obliquely excised at dorso-caudal corner and bearing there a triangular plate or keel-like lobe which lies longitudinally with the elevated end caudad; prefemur, femur and tibia longitudinally furrowed above, but the furrow of femur scarcely more developed than that of the other articles and this article not otherwise especially modified; none of articles bearing bunches of hair, the latter being everywhere sparse; tarsal joints abruptly more slender.

Gonopods of male wide, truncate distad, flattened in an ecto-ventral dorso-mesal direction; bearing a few short bristles in a row along distal edge of ventral side.

Body strongly narrowed from eighth plate forward to the first which is clearly narrower than the third; the eighth and tenth plates of equal width and much wider than the head, the latter in type being even slightly narrower than the third plate. Body about  $7\frac{1}{4}$  times longer than width of tenth plate.

Length of type (a male) 12.5 mm.; of antennæ 5 mm.; width of tenth plate 1.7 mm. Width of head, first, third, eighth, and tenth plates to each other about as 18, 17, 19, 24 and 24.

Locality: Byram, Mississippi (author, July, 1910).

In ANNALS ENT. SOC. AMERICA, 1911, p. 43 the type of the species was referred tentatively to *A. aedipes* Bollman, but study of the type of the latter shows it to be clearly distinct.

Genus *Gosibius* Chamberlin.

*Gosibius monicus* sp. nov.

Dorsum brown, with a darker median longitudinal stripe which shows a marked tendency to spread laterally at the caudal end of each plate and often reaches the lateral margins across the caudal border. Head ferruginous; the median longitudinal stripe of dorsum continuing forward upon the head as far as a little caudad of the frontal suture where it ends abruptly at a pale transverse band. Antennæ ferruginous. Prosternum and prehensorial feet pale ferruginous. Venter yellow or testaceous, the caudal segments darker, more reddish or ferruginous. Legs yellow or testaceous like the venter, nearly uniform, or the caudal pairs slightly darker dorsally.

Head subcordate, wider than long in about ratio 47: 45. Caudal margin mesally gently incurved; sides conspicuously converging from the lateral interruptions caudad about the rounded corners. A median longitudinal sulcus extending forward from frontal suture to a transverse depression between the antennæ, narrow and not very deep. A short, deep, transverse sulcus a little in front of median portion of caudal margin, the same being more weakly indicated farther laterad on each side. Smooth and shining, not punctate or roughened.

First dorsal plate smooth and shining like the head, or very obscurely roughened. Other dorsal plates more or less roughened, the more caudal ones most strongly so. Major plates with the short transverse sulcus adjacent to each lateral margin at about one-third its length from caudal end, the seventh having in addition a similar sulcus near the middle of length. A median longitudinal furrow on each side between middle and lateral margin which may be indistinct, especially on caudal portion of plate; this furrow at about beginning of middle third of length sending off a more clearly impressed branch directly mesad which may be united with the corresponding furrow from the other side; often a short sulcus running from near anterior margin obliquely ecto-caudad toward point of origin of this transverse furrow.

Ventral plates apparently smooth and shining; the usual three longitudinal impressions indicated in varying degrees of distinctness. On several of the caudal plates the median furrow may end caudad in a deeper, pit-like and somewhat transverse, depression a little in front of caudal margin of plate.

Antennæ long. In types tips are broken off so that full number of articles can not be ascertained; but the number present indicates that the full number is somewhere above 29.

Eyes in types from 15 to 17 in number, arranged in four series; thus, 1+4 (5), 4, 4, 2; 1+4, 4, 4 (3), 4.

Prosternal teeth 2+2, stout, conical, much closer together than in paucidens and also larger, but the proportion of anterior margin occupied larger than in that species. Ectal spines long and distally drawn out into slender, bristle-like, acute tip; the tubercles contiguous with outer tooth and not well removed from it as in paucidens.

Coxal pores circular, rather small; 4, 3, 3, 3, in the types.

Last four pairs of coxæ laterally armed. Spines of first legs,  $\frac{0, 0, 2, 2, 1}{0, 0, 2, 3, 2}$ ; of second,  $\frac{0, 0, 3, 2, 1}{0, 0, 2, 3, 2}$ ; of the third and fourth,  $\frac{0, 0, 3, 2, 2}{0, 0, 2, 3, 2}$ ; of the fifth to ninth,  $\frac{0, 0, 3, 2, 2}{0, 0, 2, 3, 3}$ ; of the tenth,  $\frac{1(0), 3, 2, 2}{0, 0, 3, 3, 3}$ ; of the eleventh,  $\frac{1, 0, 3, 2, 2}{0, 0, 3, 3, 3}$ ; of the twelfth and thirteenth,  $\frac{1, 0, 3, 2, 2}{0, 1, 3, 3, 3}$ ; of the penult,  $\frac{1, 0, 3, 2, 2}{0, 1, 3, 3, 2}$  armed with two (3?) claws; of the anal,  $\frac{1, 0, 3, 2, 2(1?)}{0, 1, 3, 3, 1}$ , armed with two claws. Anal legs in the female short and moderately slender, the dorsal surface of femur and tibia distinctly longitudinally furrowed, the same articles of penult legs similarly but less strongly furrowed.

Gonopods of female with the claw long and acute, strongly curved and chitinized. Proximal article excavated at base on mesal side, leaving a conspicuous lobe at distal end which projects mesad and meets the corresponding lobe of other gonopod; the caudal and mesal sides of this articles strongly chitinized as usual. Basal spines 2+2, stout, the inner smaller than the outer. Median process of sternite first clavately widening caudad, and then attenuated to a slender acute point.

Length of types 14 to 15 mm. A specimen (female) 14 mm. long has anal legs 5.8 mm. long and the tenth dorsal plate 2 mm. wide, the body being thus seven times as long as the width of this plate. The body moderately narrowed cephalad and the first plate slightly narrower than the third whereas it is wider in paucidens. The widths of head and first, third, eighth and tenth dorsal plates to each other about as 53, 47, 48, 57, and 57.

Locality: Santa Monica, California (author, June, 1909).

#### Genus *Lithobius* Leach.

#### *Lithobius devorans* sp. nov.

Dorsum from brown to chestnut and, in largest individuals in full color, almost mahogany. In lighter individuals the head is chestnut and clearly darker than the dorsal plates excepting the first in some in which it may approach the same color; in the more deeply colored individuals the head is deep chestnut or mahogany of scarcely deeper shade than that of dorsal plates. Antennæ chestnut, usually paler at very tips only. Prosternum chestnut, the prehensorial feet more rufous. Venter fulvous to brown, the caudal plates always darker and either reddish or very deep brown. Legs colored like contiguous portion of venter, the caudal pairs being thus always darker.

Head slightly wider than long (72: 70). Caudal margin straight or nearly so; posterior corners conspicuously and widely rounded, the



sides immediately in front of them but little excurved, diverging forward to the lateral interruptions which are distinct. The short curved transverse submarginal sulcus opposite interruption of each side evident. The usual semi-circular impression on caudal portion clearly marked. There is also present a transverse sulcus immediately caudal of and subparallel with frontal suture, the sulcus being most distinct at the sides. Surface sparsely punctate and moderately uneven.

Posterior dorsal plates conspicuously roughened; the anterior ones less strongly so and the first uneven only in about same degree as head. The short transverse sulci most distinctly impressed on the more caudal plates, mostly weak on the anterior ones. Caudal plates with short hairs more numerous than on the anterior. Posterior angles of the seventh, ninth, eleventh and thirteenth dorsal plates strongly produced; processes of ninth, eleventh and thirteenth long and acute, those of the seventh obtusely rounded, the inner or mesal edges being convex and long with its ectal or distal portion nearly transverse.

Anal segment in the male densely clothed above with rather long hairs, most of which are curved or uncinatate at tips, this being a very characteristic feature of the species. In the female the dorsal hairs of this segment are sparse and straight.

The three longitudinal sulci of ventral plates distinct, being on most broadly and deeply impressed to a little in front of caudal margin. Last plate more densely clothed with short hairs. Sternite of genital segment also densely clothed with hairs especially in the male.

Antennæ reaching the beginning of the eighth segment; attenuated, very slender distally. Composed of mostly from 32 to 35 articles which, distad of the first few, are rather short, considerably shorter ones occurring at intervals among longer ones as in related species.

Eyes composed of from 28 to 42, but mostly from 30 to 36, ocelli which are arranged in from 5 to 8 series; e. g., 1+3, 4, 6, 6, 6, 5; 1+3, 4, 6, 6, 6, 6, 3; 1+6, 5, 6, 5, 4, 4, 4; 1+6 5, 6, 5, 5. Single ocellus moderately large, oval. All seriate ocelli deeply pigmented excepting those of first row which are commonly paler as in related species. Of seriate ocelli the caudal ones of first row are clearly the largest.

Prosternum about 1.7 times wider than long. Distance between chitinous spots 1.8 times the width at level of bottom of mesal incision, and 2.5 to 2.7 times as great as length of dental line, the variation depending on number of teeth. Teeth 5+5 or 6+6, or occasionally 5+6; distally narrowly rounded. The prosternal spine situated immediately ectad of outer tooth as usual, slender and bristle like, and curved as in voracior.

In larger specimens the coxal pores are very large and strongly transverse, while in the smaller axults the form may approach that of the pseudomaturus stage, being transversely elliptic and with those at ends of rows often subcircular. In number and arrangement from 6, 6, 6, 5 to 8, 8, 8, 7, other arrangement noted being 6, 7, 7, 6, to 7, 7, 7, 5, and 7, 8, 8, 6.

Last three pairs of coxæ laterally armed. Spines of first legs,  $\frac{0, 0, 3, 2, 1}{0, 0, 2, 3, 2}$ ; of the second,  $\frac{0, 0, 3, 2, 1}{0, 0, 2, 3, 2}$ ; of the third,  $\frac{0, 0, 3, 2, 2}{0, 0, 2, 3, 2}$  or  $\frac{0, 0, 3, 2, 2}{0, 0, 3, 2, 2}$ ; of the fourth and fifth,  $\frac{0, 0, 3, 2, 2}{0, 0, 3, 3, 2}$  or  $\frac{0, 0, 3, 2, 2}{0, 0, 2, 3, 2}$ ; of the sixth to the eleventh,  $\frac{0, 0, 3, 2, 2}{0, 0, 3, 3, 2}$ ; of the twelfth,  $\frac{1, 0, 3, 2, 2}{0, 1, 3, 3, 2}$ , the thirteenth being the same; of the penult,  $\frac{1, 0, 3, 1, 0}{0, 1, 3, 3, 2}$  or  $\frac{1, 0, 3, 2, 1}{0, 1, 3, 3, 2}$ , the anterior or ectal dorsal spine of the fourth joint in the latter case being mostly very small, claws two or three, in latter case the anterior accessory being very small; of anal,  $\frac{1, 0, 3, 1, 0}{0, 1, 3, 3, 2}$ , the claw single.

The anal legs in the male are short. Fourth article considerably thickened, more so than in voracior; dorsal or dorso-mesal surface conspicuously bowed ventrad or depressed over middle and posterior portion, or the depression often almost strictly mesal, longitudinally furrowed along depressed surface; also longitudinally furrowed along dorsal surface toward ectal edge of latter. Third and fourth articles rather deeply sulcate longitudinally on ventral surface. Tibia longitudinally furrowed dorsally. Tarsal joints not clearly sulcate mesally. Penult legs very similar to anal but the fourth article but slightly enlarged and not at all excavated meso- or caudo-dorsally, though the dorsal longitudinal furrow is conspicuous.

The single article composing the gonopod of male well exposed; directed caudo-ectad; sides nearly parallel; distally subtruncate; bearing mostly about four bristles. In the gonopods of the female the claw is comparatively short; strongly bent; tripartite, the three lobes distinct, the median being considerably larger much as in vorax but not so greatly exceeding the lateral as in mordax, etc. Basal spines stout and moderately long; mostly uniformly attenuated from base to apex. Mesal side of first article straight, diverging cephalad from mesal side of fellow but little.

Body appearing to vary considerably in relative width, the length being mostly as much as eight times longer than width of tenth plate, but in some falling a little below this (7.75) and in others as much as 8.4 times longer. Moderately attenuated cephalad from eighth plate, with the first plate a very little wider than the third and usually a little narrower than the head, occasionally as wide as latter; the average ratio of widths of head, first and tenth plates is 30:29:35. In one male the widths of head and first, third, eighth, tenth and twelfth dorsal plates stand to each other as 72, 72, 70, 78, 78, and 72.

Length from 18 to 26 mm. A male 25 mm. long has antennæ about 12.5 mm. long, anal legs 8.5-9 mm. long and the tenth dorsal plate 2.9 mm. wide.

Locality: Jackson, Alabama (author, 1910).

This species is very close to the next, *L. voracior*. Usually both sexes of fully grown specimens of these species are to be distinguished quite readily by the form of the coxal pores,

these in voracior being circular or broadly elliptic whereas in devorans they are larger and mostly strongly transverse. In some cases, however, it is difficult to separate the females, although the males are always very readily distinguished by the character of the hair clothing the anal segment dorsally, this in devorans being long and dense with nearly all the hairs uncinata distally whereas they are all straight in the other species. Devorans averages larger. It is relatively more slender and the width of the head as compared with that of the tenth plate is as 60:70 on an average whereas the average corresponding ratio in voracior is 60:65.5

***Lithobius voracior* sp. nov.**

Dorsum brown, the first plate and the several most caudal ones commonly darker and more reddish of chestnut; plates often showing three longitudinal pale lines. Head conspicuously darker than the dorsum, cherry red or chestnut, or in others often very dark, nearly mahogany. Antennae chestnut, much lighter distad. Prosternum dark brown or dilute brownish chestnut, with the prehensors paler. Venter yellowish brown, the posterior plates much darker, burnt brown. Legs yellowish brown, the posterior pairs darker, being often somewhat chestnut with distal articles a little paler.

Head wider than long. Widest immediately back of eyes. Sides rather strongly convex and converging caudad of the well marked marginal breaks to the rounded posterior corners. Caudal margin nearly straight or but slightly incurved mesally. The usual subcircular impression on caudal portion. Surface subsparingly punctate, the punctae varying in size but mostly fine; obscurely uneven.

First dorsal plate with surface similar to that of head. All finely punctate. Plates roughened more especially the caudal ones as usual, the elevations or irregular tubercles small. Posterior angles of seventh, ninth, eleventh and thirteenth dorsal plates strongly produced, processes of the seventh much as in devorans.

Anal segment in male dorsally densely clothed with rather long and strictly straight hairs, these not being at all distally curved or uncinata. In the female the dorsal hairs of this segment are but sparse.

Ventral plates densely punctate and with numerous fine impressed lines which mostly run out from the punctae. The usual longitudinal furrows clearly developed. Hairs of posterior plates more numerous and longer.

Antennae of moderate length, reaching mostly to the end of the seventh or beginning of eighth segment. Attenuated considerably but the distal portion not very fine. Articles beyond the first several rather short. Hairs moderately long. Articles in number from 32 to 36.

Eyes composed mostly of from 30 to 35 ocelli, rarely as few as 23, arranged in from 5 to 7 longitudinal series; e. g., 1+3, 5, 5, 5, 4; 1+3, 4, 5, 6, 5, 4, 2; 1+5, 5, 6, 6, 4, 3; 1+3, 5, 6, 6, 6, 4, 3; 1+4, 6, 7, 6, 5, 4, 1.

Single ocellus large subvertically oval. Ocelli of most dorsal row larger and paler as in related species.

Prosternum 1.6 times wider than long. Distance between chitinous spots 1.9 times wider than long of prosternum at level of bottom of mesal incision; 2.3 or 2.4 times as great as length of dental line usually, this varying with number of teeth present. Prosternal teeth 6+6 to 8+8, other numbers noted being 6+7, 7+7, and 7+8; either uniform or varying irregularly in size; subacute, being but narrowly rounded at tips. Spine proximally clearly stouter than the hairs, but distally bristle-like, curved; situated immediately ectad of outer tooth.

Coxal pores transversely elliptic or in part subcircular; of medium size; in largest specimens more strongly transverse as in the preceding species. In number from 6, 6, 6, 4 to 8, 8, 8, 6, other arrangements frequently noted being 6, 7, 7, 5; 6, 7, 6, 5; 6, 6, 6, 5; 7, 7, 7, 6, and 7, 8, 8, 7.

Last three pairs of coxæ laterally armed. Spines of first legs,  $\frac{0, 0, 3, 2, 1}{0, 0, 2, 3, 2}$ ; of second,  $\frac{0, 0, 3, 2, 1}{0, 0, 2, 3, 2}$ ; of third,  $\frac{0, 0, 3, 2, 2}{0, 0, 2, 3, 2}$ ; of fourth to eighth,  $\frac{0, 0, 3, 2, 2}{0, 0, 2, 3, 2}$  or  $\frac{0, 0, 3, 2, 2}{0, 0, 3, 3, 2}$ ; of ninth to eleventh,  $\frac{0, 0, 3, 2, 2}{0, 0, 3, 3, 2}$ ; of twelfth,  $\frac{1(0), 0, 3, 2, 2}{0, 1, 3, 3, 2}$  or  $\frac{1(0), 3, 2, 2}{0, 9, 3, 3, 2}$  a spine sometimes borne by trochanter of one leg while absent from the other; of thirteenth,  $\frac{1, 0, 3, 2, 2}{0, 1, 3, 3, 2}$ ; of penult,  $\frac{1, 0, 3, 1, 1}{0, 1, 3, 3, 2}$  or  $\frac{1, 0, 3, 2, 1}{0, 1, 3, 3, 2}$ , the anterior spines of fourth joint in latter case being mostly very small, tarsi ending in three claws but the anterior accessory one mostly minute as in related species; of anal  $\frac{1, 0, 3, 1, 0}{0, 1, 3, 3, 1}$ , the claw single.

Anal legs in female short and rather slender; the third, fourth and fifth articles longitudinally sulcate dorsally, the fourth being most deeply so; the third and fourth articles sulcate ventrally. Penult legs similarly but less strongly sulcate. In the male the penult legs are as in the female; but the anal legs are more strongly modified. Fourth article with dorsal surface depressed or bowed ventrad over middle and proximal portion; relatively thicker than in female; articles longitudinally sulcate along mesal surface, especially so in the more distal ones.

Gonopods of male rather small; distally strongly rounded or broadly subconic; bearing 6 or 7 long bristles.

Gonopods of female with claw long and rather strongly bent or curved near middle; tripartite, the median division long and acute, the lateral small and also usually acute, the inner or more dorsal one considerably more distal in position than the outer one which is near the middle of length of claw. Basal spines long and stout, subequal, attenuated uniformly from base distad. Basal article with inner side nearly straight.

Body more robust than in devorans, the length being mostly less than seven times as great as width of tenth dorsal plate (6.8). Considerably attenuated cephalad from eighth plate, with the third plate narrower

than the first and the latter clearly narrower than the head. Average ratio between widths of head and first and tenth dorsal plates 68:65:74.3. A male has widths of head and first, third, eighth, tenth and twelfth dorsal plates to each other as 68, 65, 63, 75, 75, and 68.

Length from 17 to 24 mm. A female 19 mm. long has antennæ 10.5-11 mm. long, anal legs 8.5+ mm. long, and tenth dorsal plate 2.8 mm. wide. Males have similar relative measurements.

Type Locality: Fernwood, Mississippi.

Known Localities: Mississippi (Fernwood, Canton and Byram. Author, collector, 1910).

Although it has seemed impossible on the basis of any previously stated characters to maintain as distinct several species allied to *L. mordax* and *L. vorax*, through the use of characters not previously detected the writer finds it now an easy matter to discriminate between them. Such of this group of species, the larger forms dominating in the Southeast, as have the posterior angles of seventh, ninth, eleventh and thirteenth dorsal plates produced thus far known from the U. S., are, in addition to *devorans* and *voracior*, above described, the following: *mordax* K., *transmarium* K., *vorax* Meinert, *tyrannus* Bollman, *suprenans* Chamberlin, and *latzeli* Meinert. The writer's previously expressed opinion that *clarus* McNeill was based upon immature specimens has been confirmed by an examination of the types of this species, these proving to be *vorax* in the pseudomaturus stage; *mordax* and *transmarinus*, merged by Bollman in *spinipes* Say, are clearly distinct; and study of types shows *tyrannus* and *latzeli* to differ from *vorax* which previously had been thought identical, the published diagnoses revealing no truly distinctive characters.

Genus **Sozibius** gen. nov.

Type.—*Lithobius tuobukus* Chamberlin.

The following species is placed here only tentatively.

**Sozibius pungonius** sp. nov.

Dorsum very light brown. Head cephalad of frontal suture and the caudal segments darker, somewhat orange colored. Antennæ yellow. Venter and legs very pale, the posterior pairs bright yellow. Prosternum and ultimate ventral plates dark yellow.

Antennæ short composed of twenty-one articles of which the first six are long, the others shorter.

Ocelli about eleven, small arranged in three curved and rather irregular series; thus, 1+5, 3, 2.

Prosternal teeth 2+3.

Angles of none of the dorsal plates produced.

Coxal pores very small, 2, 3, 3, 2.

Ultimate pair of coxæ armed laterally, the ultimate and penult pairs armed dorsally.

Spines of first legs 2, 3, 2; of the penult 1, 3, 3, 2, the claw single; of the ultimate 1, 3, 2, 1, the claw single.

Anal legs of male long and slender the fourth, fifth and sixth joints longitudinally furrowed on ectal surface, laterally compressed.

Length.

Locality: Marshall, Colorado (Prof. T. D. A. Cockerell).

One male specimen.

Genus **Poabius** gen nov.

*Type*.—*Poabius verdescens* Chamberlin.

Other known species belonging to this genus are *bilabiatus* Wood, *pitophilus* Chamberlin, *sokovus* Chamberlin, *clavigerens* Chamberlin, *utahensis* Chamberlin, *yukus* sp. n., and the two new species described below.

**Poabius nankus** sp. nov.

Light orange brown, caudal borders of major scuta darker; head somewhat darker brown caudad of frontal suture. Antennæ and legs yellow. Venter yellow, the prosternum and caudal segments a little darker.

Body markedly attenuated from tenth dorsal plate cephalad. Most dorsal plates with a strong median furrow which may be doubled and, on each side, one or two approximate lateral ones diverging from it caudad; within each lateral margin a furrow or sulcus running from near anterior edge at first near to and subparallel with the lateral margin and then bending away from it caudo-mesad to end at the transverse furrow which traverses most plates a little cephalad of caudal margin.

Head subcordiform; caudal margin nearly straight; distinctly margined caudally and along cauda-lateral angles; a short transverse sulcus a little cephalad of caudal margin and between this and the frontal suture a median and several lateral pairs of longitudinal impressed lines or sulci.

Antennæ moderately short, composed of twenty more or less uniform articles.

Ocelli pale, small, fifteen or sixteen in number arranged in four straight and regular series; thus, 1+5, 4, 4, 1 (2).

Prosternal teeth dark, low, 2+2.

Angles of none of the dorsal plates produced.

Coxal pores circular, the edges weakly chitinized; 2, 3, 3, 2.

Last two pairs of coxæ laterally armed; the last three pairs dorsally armed.

Spines of the first legs 1, 3, 2; of the penult, 1, 3, 3, 2, armed with three claws; of the anal 1, 3, 2, 1, the claw single.

Gonopods of female with the claw tripartite; basal spines 2+2.

In the male the anal legs have the prefemur elevated into a rim-like structure on dorsal or dorso-mesal side at distal end, and the femur bears at the proximal end on same side an ear-shaped process which is

excavated above, the depression being continuous with a longitudinal median furrow on dorsal surface. See Pl. XII, fig. 4.

Length 13–14 mm.; width at tenth plate 1.9–2.2 mm.

Locality: Las Valles, New Mexico (Prof. T. D. A. Cockerell)

The types consist of a male and a female.

**Poabius iginus** sp. nov.

Light brown, scuta mostly with the caudal borders darker, reddish brown; posterior segments darker. Head chestnut, darkest behind frontal suture, a dusky or blackish median longitudinal stripe for a short distance in front of caudal margin. Legs yellowish, caudal pair from base to fourth joint inclusive reddish brown or chestnut, distally like the others. Venter brown, the ultimate plates reddish brown. Prosternum light reddish brown. Antennæ mostly dark brown, becoming pale distad.

Scuta roughened, mostly showing a median and two lateral longitudinal sulci or in some the median replaced by two diverging sulci.

Antennæ moderate, articles 20.

Ocelli distinct, ten in number, arranged in three series; thus, 1+4, 3, 2.

Prosternal teeth 2+2.

Angles of none of the dorsal plates produced.

Coxal pores small, well separated, round, 2, 3, 3 (4), 2.

Last two pairs of coxæ laterally armed.

Tarsi of anterior pairs of legs rather indistinctly biarticulate. Spines of first legs 2, 3, 2; of penult 1, 3, 3, 2, armed with three claws; of the anal 1, 3, 2, 0, the claw single.

Gonopods of female with the claw tripartite; basal spines 2+2, proximally clavate, distally conical.

Anal legs of male with the fourth joint enlarged and bearing meso-dorsally and proximad of middle a conspicuous, flattened, keel-like lobe and at its distal end a small wart-like elevation.

See Pl. XIII, fig. 2.

Length 11.5 mm.; width 1.7 mm. Length of antennæ 4 mm.; of anal legs 4.2 mm.

Locality: Madison, Wash. (Dr. E. Bergroth).

Closely allied to *P. bilabiatatus* and *P. verdescens*; but manifestly smaller and differing in the lobes of anal legs and in the smaller number of spines born dorsally at distal end of third joint, etc. See Pl. XIII, figs. 1 and 2.

Family CRYPTOPIDÆ.

Genus **Kethops**, gen. nov.

Pairs of legs 23.

Seventh segment not bearing spiracles.

First dorsal plate with transverse semi-circular sulcus.

Other dorsal plates excepting the ultimate with two sharply impressed longitudinal and subparallel sulci.

Last dorsal plate margined laterally, caudal margin convexly protruding.

Sternal plates elongate, narrowed caudad the caudo lateral corners obliquely excised. (See Pl. XIII, fig. 5). Each with a distinct longitudinal median sulcus and submarginal sulci.

Pseudopleura produced caudad into an acutely pointed process; porose ventrally; armed ventrally and laterally with spines.

Legs sparsely armed with spinescent bristles which appear spine-like especially on proximal joints. A stout spine at distal end of tibia dorsal in position and a second one ventral. Tarsi, excepting the ultimate, one-jointed, a stout ventral spine distad of middle.

Prefemur of anal legs armed with rows of spines on mesal and ectal surface and on most of the ventral. Femur similarly armed mesally and ventrally. The tibia with similar spines ventrally. Tarsus composed of but two joints and ending in a distinct and very stout claw.

Type: *Kethops utahensis* Chamberlin.

The type species was originally described from Utah under the genus *Newportia*, the absence of anal legs from the type specimen leading to the reference to this genus. While close to *Newportia*, it has various *Cryptops*-like characters and is readily separated by the character of the anal legs, etc. A short time ago among some old material from New Mexico sent me by Prof. Cockerell, a perfect specimen of the form was found, making possible the diagnosis given above. A description of this specimen follows:

***Kethops utahensis* Chamberlin.**

Ferruginous, uniform; antennæ and legs, excepting the ultimate pair, paler, yellowish; anal legs colored like the body, but pale distad.

Head coarsely punctate, two diverging longitudinal sulci on the caudal portion which begin at a transverse sulcus in front of and parallel the caudal margin.

Antennæ composed of seventeen articles.

First dorsal plate with semi-circular impression deep, somewhat angularly bent caudad at middle, mesal portion in a broad depression or pit on the caudal slope of which there is a distinct W-shaped mark like that found in many species of *Newportia*, the two usual longitudinal sulci over caudal portion of plate.

Sulci of second plate strongly diverging caudad, those of the succeeding plates nearly parallel.

Last dorsal plate without distinct sulci; caudal margin convexly bowed out; lateral margins armed with two rows of spinules. (See Pl. XIII, fig. 3).

Anterior margin of prosternum straight or nearly so, but slightly indented mesally. Prosternum punctate, two sulci, which, approximate below, diverge distad toward the free margin.



Ventral plates irregularly punctate, more densely so on caudal portion. Median sulcus beginning a little caudad of anterior margin and extending over anterior two-thirds or somewhat more of length of plate; a submarginal sulcus on each side which is deepest mesally; usually two or more weaker and more indefinite transverse sulci as shown in the figure. (See Pl. XIII, fig. 5).

Last ventral plate narrowed caudad; rounded caudally; bearing spinules over entire surface.

Last pleuræ furrowed laterally; with numerous small pores on ventral surface, both the free portion and that covered by ventral plate. Caudal process bearing acute spine distad. Pleuræ with many spines laterally and ventrally. (See Pl. XIII, fig. 4).

Prefemur of anal legs longitudinally furrowed both ventrally and dorsally; armed with numerous spines arranged in obliquely longitudinal rows which cover entire surface excepting dorsal portion and the furrow on the ventral. Femur also longitudinal furrowed dorsally and ventrally, the mesal side of ventral furrow formed by a keel-like elevation which does not quite reach distal end. Spines on edge of keel and elsewhere on ventral surface as shown in figure. Tibia with a mesally bent longitudinal keel, the bent mesal portion lower than end parts, this keel limiting a broad groove mesally, into which groove the tarsi of the specimen are bent or flexed like the blade of a knife. First joint of tarsus with at least one ventral spine; claw long and stout.

Length about 20 mm.

Locality: Glorieta, New Mexico (Prof. T. D. A. Cockerell).

The original type was collected by the author at the Warm Springs north of Salt Lake City in 1908.

Family SCOLOPENDRIDÆ.

Genus *Scolopendra* Linn.

*Scolopendra mohavea* sp. nov.

Very pale olive brown; the caudal half of body darker brown, dusky, or in one specimen largely solid black, with a pale longitudinal median line, Head paler cephalad of frontal suture.

Head with a transverse sulcus a little ways in front of the caudal margin, and between this sulcus and the caudal margin two straight, short, longitudinal sulci which are parallel. Cephalad of transverse caudal sulcus a pair of furrows which converge forward and end caudad of frontal suture, each furrow doubly curved, at caudal portion with concavity ectad, anteriorly convex ectad, the very anterior end bent abruptly mesad; ectad of each one of these furrows a second less sharply impressed furrow which also converges toward the mesal line cephalad; between the two sulci on each side a short sulcus runs obliquely cephalo-ectad. Smooth.

Antennæ long; composed of twenty-six articles of which the first six or seven are comparatively smooth, the scattered hairs upon them increasing on number from the first article distad.

First dorsal plate with sharply impressed cervical furrow. On each side a furrow which caudad is parallel with caudal margin, from there curving obliquely cephalo-ecta. A median longitudinal sulcus cephalad of cervical groove. Smooth.

Second dorsal plate with median longitudinal sulcus on anterior half. The two usual paired sulci crossing the entire plate and diverging caudad. On each caudo-lateral portion of plate a furrow curving obliquely cephalo-ectad as on first plate, similarly taking its origin near caudal margin.

Third and fourth dorsal scuta with median furrow. The paired longitudinal sulci less strongly diverging caudad than on preceding plate. Furrow on each caudo-lateral portion as in the preceding scuta.

On the fifth and subsequent dorsal plates the paired sulci become nearly parallel, but diverging some at the ends. Median furrow evident, but not so the caudo-lateral ones. On each side a longitudinal furrow subparallel with the lateral margin, this furrow often broken. On a few of the more caudal segments a transverse sulcus on each side parallel with and close to the anterior margin. The twentieth plate laterally margined for its entire length; the nineteenth all but a short distance caudad; the eighteenth not margined for a somewhat greater distance caudad and a short distance cephalad; the margination of the seventeenth and sixteenth plates similar to eighteenth but extending less caudad and cephalad reaching the transverse sulcus; other plates not margined.

Last dorsal plate with caudal margin mesally strongly and evenly convexly extended. A sharply impressed longitudinal median sulcus which does not quite reach the caudal margin. A short furrow parallel to the median one opposite its middle portion on each side.

Prosternum smooth; a median sulcus evident only for a short distance distad; transverse sulcus obscure; two weak longitudinal furrows, which, close to the mesal line caudad, diverge and are more distinct cephalad. Each dental plate with four teeth, of which the three inner ones are basally fused, the two most mesal being free only at their distal points; a deep narrow incision between the plates; the transverse furrow at base of each plate distinct, the two meeting mesally at an obtuse angle.

Basal tooth of prehensorial feet long, subacute, presenting but one point.

Penult article of palpus of second maxilla with a slender spine at distal end.

Ventral plates from the second to the twentieth inclusive with two sharply impressed longitudinal sulci which cross the entire plate.

Last ventral plate narrowed caudad, the sides weakly excurved-caudo-lateral corners rounded; caudal margin a little incurved mesally. Smooth. Depressed along the median line. A weak furrow subparallel with and not far from each lateral margin.

Prefemora and femora of legs of the first to penult pair inclusive without any dorsal spines at distal end; all with a tarsal spine, those of the first pair with two.

Pseudopleura ending in a stout process which terminates in two points or spines and bears proximad on its ectal surface a row of three stout teeth or spines.

Prefemur of anal legs ventrally with seventeen spines arranged in three longitudinal rows, of which the innermost is proximally irregular; these from ectal row mesad arranged thus, 4, 6, 7. Mesal surface with ten spines. Distal process with five spines. Femur unspined. Claw of tarsus with two basal spines.

Length 40-45 mm.

Locality: Fort Mohave, Arizona (March 7 and 18, 1911).

Three specimens received from Prof. Junius Henderson of the University of Colorado Museum.

Family SONIPHILIDÆ.

Genus *Soniphilus* Chamberlin.

*Soniphilus geronimo* sp. nov.

Yellowish brown anteriorly, becoming clearer yellow caudad. Head darker caudad of frontal suture. Antennæ light brown, paler distad. Legs yellow, those of anterior segments darker. Prosternum and prehensorial feet light reddish.

Antennæ of moderate length; articles moderate, not much differing in length, the ultimate about equal in length to the two preceding taken together.

Cephalic plate longer than wide in about ratio 7:6; narrowed cephalad; lateral and anterior margins convex, the latter a little emarginate mesally; middle portion of caudal margin sub-straight, rounded laterally. A short impressed median line back frontal region; on each side a little mesad from and parallel with margin a longitudinal furrow; on lateral portion of plate on each side a pair of sulci diverging cephalad and a second less distinct pair more mesal in position. Frontal plate not discrete. (See Pl. XII, fig. 4.)

Labrum with median piece comparatively large, bearing about six stout teeth.

Prebasal plate not exposed. Basal plate short, its greatest width more than 4.5 times the median length, a greater length exposed on each side. (See Pl. XII, fig. 4.)

Claws of prehensorial feet when closed not reaching anterior margin of head by a considerable distance. None of the joints bearing teeth or nodules. (See Pl. XII, fig. 2.)

Dorsal scuta with lateral sulci distinct; a second pair of sulci close to median line and on most also an intermediate sulcus on each side.

Anterior prescuta very short, increasing in length to about beginning of caudal third, then again more rapidly decreasing and becoming again short.

Anterior spiracle moderately large, circular or subcircular, being slightly vertically elongate; succeeding spiracles all circular, very gradually decreasing in size to the caudal ones which are very small.

First pair of legs much shorter and more slender than the second.

Ultimate legs long, the penult and antepenult joints furrowed longitudinally on ventral surface. Claw long and stout.

Sterna with a distinct median longitudinal sulcus or furrow which is crossed at middle by a transverse furrow. Pores not detected.

Last ventral plate very wide, strongly narrowed caudad. Caudal margin straight or a little incurved. (See Pl. XII, fig. 3).

Anal pleuræ bearing a number of small pores which are all wholly covered by the last ventral plate.

Anal pores not detected.

Pairs of legs 73.

Length 34 mm.; width 1 mm.

Locality: San Geronimo, New Mexico, (Mrs. W. P. Cockerell and Miss Mary Cooper, coll.).

#### CLASS DIPLOPODA.

##### Family NANNOLENIDÆ.

##### Genus *Buwatia* gen. nov.

Ocelli none.

Antennæ clavate, the fifth and sixth articles thickest; third and fifth longest, nearly equal in length, the second and fourth next.

Body decidedly narrowed caudad of head to sixth segment.

Body iulus-like in form. Segments without carinæ, nearly smooth, not clothed with hair. All segments striate beneath; a deep sulcus across segment at level of pore.

Claws of legs long and slender.

Type: *Buwatia monterea* sp. nov.

As but one specimen of the type species has been secured, dissection for fuller structural details has not as yet been attempted. The genus may be distinguished from *Nannolene* through the absence of ocelli.

##### *Buwatia monterea* sp. nov.

Dorsum brown; head and anterior part of first segment whitish brown; first and ultimate segments light brown; a series of small, largely obscure dark spots along each side, one at each pore. Legs and antennæ pale.

Body slender, nearly uniform in width for most of length but decidedly constricted from head and first segment to region of sixth segment.

Head nearly smooth, weakly and very finely punctate; glabrous except for a few bristles on clypeal and labral region. A weak median longitudinal sulcus across vertex. A furrow or excavation from base of each antenna caudad to lower margin of first dorsal plate, the antenna bent back and lying in this furrow.

Antennæ rather short, strongly clavate; the seventh article short, its four sensory cones almost concealed in the terminal pit; clothing of hair becoming more and more dense distad, sparse proximad.

First dorsal plate large, closely embracing caudal portion of head. Anterior and posterior lateral angles rounded, the lateral margin between them extending obliquely caud-oventrally, rather, long, somewhat incurved. Anterior margin incurved at middle curving out convexly on each side and then again at sides incurved bow-shaped. A fine transverse sulcus subparallel to the anterior margin and some distance from it and a second one submedian in position.

Subsequent segments with a longitudinal furrow at level of pore, this more distinct on cephalic portion of segment. A transverse sulcus in front of median suture. Prozonites striate throughout, the main segment strongly striate beneath and on sides below level of pores. Dorsum a little depressed; a weak longitudinal depression each side of middle, leaving mesal portion a little elevated.

Anal scutum considerably exceeded by the anal valves; caudal division short, widely and evenly rounded, set off or limited from major portion in front by a transverse sulcus. Caudal margin with two pairs of long setæ.

Anal valves elongate, their free margins elevated. Each valve bears near its mesal margin a long seta at caudal and second one near middle of length in a furrow or sulcus which curves from mesal margin first laterad and then latero-cephalad.

Anal scale very short; caudally weakly convex, anteriorly strongly so; antero-lateral angles rounded, but not so the caudo-lateral ones.

Legs moderately long and slender; claws long, not robust.

Segments of body forty-five.

Length 11-12 mm.; width as .5-.5 mm.

Locality: Pacific Grove, Cal. (April, 1911, author.)

One specimen secured under a stone in an open field near the Hopkins Laboratory.

#### Family CAMBALIDÆ.

#### Genus *Titsona* gen. nov.

Eyes well developed, each consisting of a number of ocelli arranged in a single series parallel with anterior margin of the first dorsal plate.

Antennæ short, very slender proximad but strongly enlarged distad, clavate; the fifth and sixth articles conspicuously and abruptly thicker than others. The third, fifth and sixth articles longest, not much differing in length from each other; second and fourth articles subequal.

Gnathochilarium nearly as in *Paiteya*. Promentum triangular, completely separating the laminae linguales which are attenuated proximad to an acute angle. Mentum large, widening proximad.

Body strongly constricted from head and first segment to region of fifth and sixth segments, from where it again increases in width caudad.

First dorsal plate very large, extending over caudal portion of head from which the lateral portions extend free.

All segments striate beneath. Each segment from the fifth to the antepenult inclusive with four carinae, a dorsal carina each side of median line and one farther laterad on each side, the latter bearing the pore.

Legs sparsely armed with spinescent bristles. First pair in male reduced, composed of six articles normally armed.

*Type:* *Titsona sima* sp. nov.

Evidently close to *Paiteya*, the type of which is likewise a Californian species.

***Titsona sima* sp. nov.**

General color caudad of fifth segment dark brown, the caudal portion of each segment light brown. First dorsal plate light brown, a dark stripe parallel with but a little removed from the caudal and the cephalic border, the two stripes confluent at the sides of plate. Second to fourth segments light brown, each with a narrow transverse stripe of dark brown and especially laterally with a network of lines of same color, the proportion of dark larger the more caudal the segment. Head light brown, darker adjacent to first dorsal plate; on clypeus a square with upper side missing outlined in dark brown and immediately above this a subelliptical outline in same color with dorsal and ventral ends acutely angular. A pair of somewhat confluent brown spots in line from the brown about each eye ventro-mesad toward lower part of elliptical outline of front. Legs very pale.

Ocelli in a single row, 5-7 in number, black, uniform; the series parallel with margin of first dorsal plate which partly covers it on caudal side.

Antennae short, strongly clavate; the fifth and sixth joints much stouter than the others, the fifth strongly enlarged from its base distad, the sixth more uniform and broadest proximad. Hairs more dense distad as usual. (See Pl. X, fig. 5).

Stipites of gnathochilarium inclusive of processes nearly four times as long as greatest width. Mentum abruptly narrowed at distal end, wider at base than the median length approximately in ratio of seven to six. A semi-circular impression on proximal portion deeply impressed, the concavity directed distad. Promentum narrowly triangular. Laminæ linguales narrowed to an acute angle proximally, about three times as long as greatest width.

First dorsal plate very large, embracing caudal portion of head mesally, its lateral wings separated from sides of head by a space into which the antennae may be bent back. Anterior margin widely weakly concave, laterally running obliquely caudo-ventrad. Caudal margin nearly evenly convexly rounded mesally, lateral portion of plate bent ventrad and somewhat caudad and then mesad beneath. Caudal portion of plate more constricted than the anterior. On each side above lateral angle are several striae extending from caudal margin cephalad.

Next three segments striate beneath. Fifth and subsequent segments with prozonites striate throughout, the main division of segment striate beneath and dorsad only about half way to pore-bearing swelling

or carina. Each segment from the fourth to the antepenult with four carinae, one far dorsad on each side consisting of a hemispherical swelling chiefly on portion cephalad of suture and bearing the pore, the other close to the mesal line and also more thickened cephalad than caudad, low, rounded. All segments constricted dorsad and cephalad from the transverse suture. (See Pl. X, fig. 6).

Anal scutum long, widely rounded caudally; a rather weak median longitudinal sulcus on anterior portion; a bristle borne each side of mesal line near middle of length, and a second pair borne on caudal margin.

Anal valves long, about equalling the anal scutum; smooth; margins elevated; bearing two pairs of bristles close to mesal margin, one pair caudal and the other submedian in position.

Anal scale short and broad, transversely narrowly elliptical. A pair of bristles borne on caudal margin, one each side of mesal line.

Legs rather sparsely provided with short spinose bristles.

First legs of male reduced, six jointed.

Gonopods of male reduced and nearly wholly concealed.

Segments ad forty-two.

Length about 16 mm.; greatest width 1 mm.

Locality: Oroville, Cal. (April, 1911; author coll.).

Two specimens were secured.

#### Family NEMASOMIDÆ.

#### Genus *Nemasoma*.

#### *Nemasoma uta*, sp. nov.

Dorsum dark brown, the color nearly solid in band on caudal portion of each segment and in some in a narrower stripe adjacent to anterior margin, the color over remaining portion of segment mostly in a network or areolation over a light background, the light spots often confluent dorsally into transverse band. Sides light brown, the light area extending farthest dorsad at middle of segment, the light area of sides limited on all sides by border of dark brown. Each segment with whitish spot on median dorsal line. Vertex of head areolated with lines of dark brown over a light background, the frons between bases of antennae and the eyes dark brown, the area enclosing a pair of lighter spots each side of the median line and ventrad of these a second pair of spots between bases of antennae at lower portion of the area. Clypeal region paler from presence of numerous lighter spots, ventrad and laterally yellow, as is also the lateral portion of head. Stipes of mandibles laterally covered with network of dark brown lines over light background. Eyes deep black. Antennae brown, each segment whitish proximally and the second article almost wholly so. Legs brown, more or less broken with whitish, paler proximally. Ventral surface light brown. Anal scutum very dark, the anterior portion with numerous light dots. Anal valves pale along mesal border, elsewhere brown.

Body very slender, attenuated cephalad, narrowest immediately caudad of head.

Head smooth, free from hairs except for the usual bristles along labrum. A transverse sulcus between eyes, each side portion bending caudad to meet other at an obtuse angle on mesal line, to which angle the median longitudinal sulcus across vertex extends.

Antennæ longer than width of body; strongly clavate; sensory cones long. Subdensely hirsute distally, more sparsely proximad.

Eyes large, oblong, its upper and lower margins nearly parallel, the mesal convex and the ectal oblique. Ocelli arranged in five series; thus, 3, 4, 4, 4, 2, giving a total of 17.

First dorsal plate narrower than the head inclusive of mandibles, shorter than the two succeeding plates taken together. Middle portion of anterior margin evenly convex, laterally extending obliquely caudo-ventrad and somewhat concave. Caudal margin mesally straight, on sides convexly bending cephalad and meeting anterior margin at an angle. Dorsal of each lateral angles the plate is obliquely depressed or shallowly furrowed.

Subsequent segments smooth above; striate ventrad of level of pores, the lower or ventral striæ deep.

Anal scutum in outline as viewed from above with lateral margins parallel or a little diverging caudad, nearly straight or slightly convex; caudal margin widely rounded, bearing beneath a seta on each side. About equalling the anal valves or a little exceeded by the latter.

Anal valves strongly bulging from base to free mesal edge, the surface of each valve extending very obliquely ventrad. A long bristle borne near mesal edge of each valve near middle of length.

Anal scale with anterior and cadual margins each strongly convex, the two meeting on each side in an acute angle. A pair of bristles springing from mesal portion.

Number of segments 44.

Length 12.5 mm.; greatest width ad .75 mm.

Locality: Little Willow Canyon, Salt Lake County, Utah. (1905; author, coll.).

But one specimen thus far found.

Family PARAIULIDÆ.

Genus *Paraiulus*.

*Paraiulus tivius* sp. nov.

Head light brown, a broad transverse band between eyes and ventrad of their level deep brown, the band enclosing above two pairs of light dots, and between antennæ a pair of large obliquely placed, oval light spots, a bristle inserted in each of most dorsal pair of light spots; vertex above the dark band with network of dark lines, a similar network covering the stipes of mandibles laterally, each of the latter with dark transverse stripe across dorsal part. Ventral surface and lower part of sides of body light brown. On each side a series of black dots extending from sixth segment to about the antepenult. Anterior and caudal margins pale, adjacent to the pale marginal stripe in each case a dark transverse band which is much widest mesally; remaining part of plate



broken into network or areolation by light spots which may be confluent into one or more cross stripes. Other segments with the caudal transverse stripe, this becoming broader on more caudal segments and extending on each side to the lateral dark spot, below which it is continued as a more obscure band formed by network of dark lines, the dark band transversely divided by a series of light spots. Prozonites light brown. Anal scutum uniform dark brown, with anterior border pale. Legs light brown or yellowish. Antennæ with proximal portion of each segment yellowish, the distal darker brown, especially in ultimate articles.

A broad transverse depression extending between eyes, in its mesal portion or adjacent to same lying the setigerous light spots above mentioned. A median longitudinal sulcus crossing vertex and ending in the transverse furrow. Head nearly free from ordinary type hairs excepting the two setæ mentioned and the bristles on clypeus and labrum. On lateral portions of clypeus and on the stipes of mandibles is a number of peculiar, probably sensory, hairs, each of which is sub-clavate in form with a narrow apical process and a slender basal stalk inserted in a corresponding pit, near the upper portion of which it presents a globose enlargement. (See Pl. XI, fig. 7). The tegument about the basal stalk dark.

Eyes triangular, an angle directed toward base of antennæ, upper side straight, outer side convex above and concave below, mesal side concave above and convex below. Ocelli about 45 in 7 or 8 series; counting from above ventral, 8, 10, 8, 7, 5, 4, 2, 1.

Antennæ rather short, conspicuously clavate.

First dorsal plate with lateral borders rounded anteriorly, not produced, angular posteriorly; margined anteriorly and laterally, the elevated anterior margin widest mesally, not margined caudally. One or two rather weak striæ on each side below extending from caudal margin cephalad part way across plate.

Pores moderate, widely separated from the transverse suture which is straight or at most weakly sinuate at their level.

Anal scutum with caudal portion subtriangular as usual, the apical process bluntly rounded and not at all decurved; plate crossed by a series of transverse furrows or sulci of which the more caudal ones are deepest; caudal triangular portion of plate with a series of setæ along each lateral margin, three similar long setæ springing from caudal process. Lower portion of segment bearing a long seta near middle height of caudal margin and a second in line with legs of more anterior segments.

Anal valves nearly smooth, the mesal margins strongly elevated as usual; two setæ on each valve just ectad of elevated mesal margin, one submedian and the second between this and the caudal end.

Anal scale with anterior margin convex, the posterior portion subtriangular its sides convex. A long seta borne on margin each side of mesal line. A dark line paralleling margin but indented mesally gives superficial appearance of caudal emargination to scale.

The gnathochilarium of the male has the promentum very large, broadly elliptical in outline. For form and relations of stipes and other parts see Pl. XI, fig. 6.

First legs of male strongly enlarged, uncinatè, as usual; caudal surface glabrous excepting distal article, the anterior surface with long stout hairs. (See Pl. XI, fig. 5).

Second legs as usual greatly reduced excepting for the strongly enlarged coxæ; the latter produced mesally into a long, tongue-like process which extends cephalo-ventrad between the first legs. (See Pl. XI, fig. 4).

Gonopods large and conspicuously exposed, bent above base strongly ventro-cephalad. Inner branch of anterior pair much longer than the outer, contiguous with each other mesally, clavately enlarged distad; outer branches broad, plate-like, densely clothed with long setæ along anterior-ventral and distal borders. Anterior pair apically terminating in two spines, the more anterior of which is a little curved distad and at end is expanded; the other process strongly curved ventro-ectad, crossing the first, and terminating acutely. (See Pl. XI, figs. 1 and 2).

Length ad 20 mm.; width 1.6 mm. (female). Male more slender, length 16-18 mm.; width 1.2 mm.

Locality: Mill Valley, Cal. (April 8, 1911; author, coll.).

About a dozen specimens were secured.

#### ***Paraiulus timpius* sp. nov.**

Dorsum with a broad band of light brown, paler than the sides. A median dorsal line of black which expands into a wider dot on anterior portion of each segment. Each segment bordered caudally with a narrow blackish stripe; a broader and more diffuse transverse dark band farther cephalad on segment, this band embracing a transverse row of four light spots of which the two inner ones are smallest, oblong and obliquely placed, sometimes confluent ephcalad with anterior pale portion of segment, the two outer light spots confluent caudad with the pale area between the two dark bands. On the anterior segments the light and dark areas of dorsum merged and the whole covered with a close network or areolation of dark lines over light ground and the median dorsal line as such less distinct. First dorsal plate entirely covered with similar network, the lower portion of sides dark brown or smoky; a narrow dark transverse stripe caudad of anterior margin. Sides of segments dusky or blackish, darkest along caudal margin, in a stripe continuous with the dark dorsal one, prozonites paler; a large light spot below level of pore on each segment, this spot mostly more or less constricted into two or three parts. Venter pale, a large light spot ectad of legs on each segment. Vertex of head with a dense network of black enclosing rows of very small, longitudinally oval light dots; frons between eyes solid black, enclosing a pair of light dots close to mesal line; brown between antennæ the area enclosing a number of paler dots. Clypeal and labral region yellowish. Antennæ deep purplish brown. Legs very pale, distal joints streaked with purplish or purplish brown.

Head finely roughened or rugose; free from hairs excepting the usual ones in clypeal and labral region and a single long median bristle at anterior end of the distinct median sulcus of vertex. A deep furrow extends from mesal angle of each eye to that of the other, the furrow angularly bent caudad mesally, the longitudinal median sulcus of vertex meeting this angle; farther forward a second transverse furrow, in front of which the head appears to bulge in a low transverse ridge.

Eyes large, triangular, its sides a little convex, one angle mesal and another immediately above base of antennæ. Ocelli about 39, arranged in seven transverse and gently curving series; thus, 8, 8, 7, 6, 5, 3, 2.

Antennæ moderate; proximal joints slender; distad thickened, clavate, as usual.

First dorsal plate large; mesal length about equalling that of two succeeding segments together. Anterior margin evenly convex; cephalo-lateral corners strongly rounded, the caudo-lateral more angular. Margined laterally and at sides cephalically, but not so the median portion; caudal border not margined. Not striate on sides below. A fine median longitudinal impressed line extending from caudal margin cephalad about three-fourths of the length of plate, at its anterior end breaking into two lines which diverge cephalad and become indistinct.

All subsequent segments striate beneath and over lower portion of sides, the striae deep.

Anal scutum rounded caudad, mesally weakly indentate, a slight tooth each side of indentation; smooth.

Anal valves smooth, the mesal margin but weakly and narrowly elevate.

Anal scale with caudal margin convex, the cephalic more strongly so, the two meeting at an angle on each side. A pair of caudally projecting bristles inserted a little in front of caudal edge.

Mandibular stipes considerably produced below, mesally excavated.

Gnathochilarium with the enlarged promentum narrowly elliptical or rather wider distad than proximad as shown in figure; relatively narrower than in most species. (See Pl. XI, fig. 8).

First legs of male strongly enlarged and uncinatè in the usual way; mesal surface complanate and strongly tuberculate, the tubercles in distinct cross series. Caudal surface glabrous, long hairs on the anterior.

Second legs with the greatly enlarged coxæ fitting closely against bases of first legs and bent cephalad between the latter; other joints greatly reduced the ultimate densely clothed with short stiff hairs, those at apex longer.

Gonopods of male large and conspicuously exposed. Anterior pair with two main branches, the outer of which is flattened ect-mesally, of nearly uniform width, distally rounded, clothed with long bristles on mesal side; the inner branch also flattened or plate-like, bent cephalad and, as seen from ventro-caudal aspect, appearing expanded at free end into a foot-like shape with the toe mesal and the heel ectal in position. Each of the posterior gonopods enclosed or embraced at base on ectal side with a low plate the extended ends of which bend about it in front

and behind; an inner process which is a narrow thin plate for most of its length, terminating apically in a slender spine which curves cephalad in a sort of hook; outer division consisting of a long slender style or spine which is bent apically and ends acutely, this lying against a twisted plate-like division which at its end is sharply bent about the styliform division some distance below the end of the latter. (See Pl. XI, fig. 9).

Number of segments 46.

Length about 18 mm.; width 1.8 mm. (male).

Locality: Las Valles, New Mexico, (Prof. T. D. A. Cockrell, coll.).

A male and female are in the collection, the description above being that of the male.

***Paraiulus garius* sp. nov.**

Head with brown band bordering labial and clypeal margins, the lower mesal portion of the clypeus being pale, its upper portion of same color as the border but not solid, the dark color a mottling or network over a paler background; a black transverse band between the two black eyes, this band concavely excised on front each side of middle and enclosing a pair of small light spots near median line; vertex of head covered with close network of black or deep brown color over a lighter background, a similar or somewhat paler network covering the stipes of mandibles laterally. Antennae dark purplish brown or blackish. Body dark or dusky brown the lower portions of sides and the venter paler; a continuous dark median longitudinal line along dorsum and a row of black dots along each side beginning at about sixth segment; a darker ring of more solid color about anterior portion of each segment; a sub-circular patch of closely placed light dots on lower portion of each segment, and between this patch and the black dot an elongate patch similarly formed, while dorsad of the black spot is a third area and between the latter and the mid-dorsal line and elongate narrow band or line of such light dots; caudad of the latter line and parallel with it is a light line or narrow band partly encircling the segment but fading out ventrad on each side, this light line being continuous, not broken into dots. First segment dark along both anterior and posterior borders. Anal scutum dark brown, the vantro-caudal margins pale. Anal vales with cephalic portions dark brown, the meso-caudal portions light. Legs proximally clear yellow or light brown, the distal articles covered with network of dark purplish brown.

A deep transverse furrow between mesal angles of eyes, to which the median longitudinal sulcus across vertex extends. A row of setae along labral margin as usual and also a second row of about nine short setae across lower portion of clypeus, the latter row being inversely V-shaped with the angle very obtuse.

Antennae of moderate length, slender, not strongly clavate.

Lateral borders of first dorsal plate not produced; ventro-caudal angle in outline sub-rectangular, the vertex rounded, the margin from here running obliquely cephalo-dorsad; anterior margin widely rounded,

the caudal nearly straight, both margined, more strongly so ventrad over lateral portions. Two deep longitudinal striæ across plate dorsad of lateral margin on each side.

Segments deeply striate beneath and on lower sides, the striæ on some anterior segments extending dorsad nearly to the black spot.

Repugnatorial pores moderate, well separated from the transverse suture which at this level is very weakly curved, remaining almost straight.

Anal scutum with apical process straight, acute, not at all decurved, somewhat exceeding the anal valves; bearing four setæ along each caudo-lateral margin. (See Pl. XII, figs. 6 and 7).

Anal valves with mesal margins elevated, the elevated ridge crossed by a series of transverse sulci; each valve widely depressed caudad of and not quite parallel with the margins of anal scale. Each valve bearing two setæ ectad of elevated mesal border, one at about one-third the distance from each end. (See Pl. XII, fig. 6).

Anal scale with caudal margin subsemi-circular, the lateral angles a little extended; anterior margin widely convex. A little cephalad of caudal margin two pairs of setæ borne on tubercles. (See Pl. XII, fig. 5).

Appendages of the second segment in female consisting of a plate presenting on each side a caudo-ventrally directed lobe which in lateral aspect appears clavate and is densely covered with bristles. Springing from the anterior portion of segment between the folds of plate is a pair of very small leg-like appendages distinctly jointed and terminating in a straight transparent claw; these appendages strongly suggestive of homology with the anterior pair of ordinarily ambulatory appendages of other segments. (See Pl. XII, fig. 8, a drawing from lateral and somewhat anterior direction of a specimen in which the first segment has been partly separated from the second the better to expose the parts; a leg of first segment is shown at left.)

Segments 52.

Length ad 31 mm.; width 2.2 mm. (female).

Locality: Tolland, Col. (Elevation, 8,000 ft.). Two female specimens collected by Prof. Cockerell in Aug., 1911.

#### Family POLYDESMIDÆ.

##### Genus *Polydesmus*

##### *Polydesmus bonikus* sp. nov.

Dorsum appearing dark brown from a close network of dark reddish brown lines over a ground of light brown; prozonites light brown; a black median dorsal line which is most distinct posteriorly. Head mostly light brown, mandibles and lateral portions palest, median portion covered with areolation of dark brown lines, a dark reddish brown band across region dorsad of level of antennæ, and extending ventral in tongue-like form between the latter. Antennæ light. Venter yellowish, with some parts tinged with pink. Legs yellow, commonly tinged with pinkish distad.

Body with sides almost parallel for most of length, attenuated anteriorly and the last few segments also attenuated in the usual way.

Vertex crossed by a deeply impressed sulcus which ends abruptly in a very short transverse line above dorsal margin of the dark transverse band. Head clothed with intermixed long and short setose hairs which are densest over frontal and clypeal region.

First dorsal plate a little wider than head inclusive of mandibles. Anterior margin weakly convex, meeting the lateral margin on each side at an obtusely rounded angle, the anterior and lateral margins together roughly hemispherical; anterior and lateral borders transparent, distinctly margined. Each lateral margin obtusely incised at a point about one-third the distance from the caudo-lateral angle to the antero-lateral, but no teeth present. Caudal margin concave mesally and convex at each side, bow-shaped. Depressed longitudinally each side of median portion which appears elevated, more especially so caudad.

Second dorsal plate with lateral portions moderately bent cephalad touching or a little overlapped by the first plate. An acute tooth at antero-lateral angle; a little caudad of this a lower, very obtuse denticulation and half way between this and the caudal angle a third very weak or obscure denticulation. A broad longitudinal depression or furrow on each side somewhat less than half the distance from middle to lateral margin of plate. Tubercular areas very weakly developed, plate being nearly smooth.

Third plate very similar to the second but the lateral margins a little shorter. Caudo-lateral corner sub-rectangular, a little obtuse. Lateral teeth as on the second.

Fourth plate with lateral margin much longer than that of second and third plates. First and second denticulations smaller; antero-lateral angle well rounded.

Subsequent dorsal plates similar to the fourth. All with the lateral longitudinal depression as described for the second. Transverse sulcus weak. Distinctly margined caudally and laterally and along free portion anteriorly. The lateral denticulations very small; a fourth weak denticle appearing on some plates caudad of the third. Caudo-lateral angles becoming in posterior segments moderately produced caudad.

Anal scutum with process obtusely rounded and bearing long setæ. Dorsally with conical setigerous tubercles.

Anal valves broad, rounded laterally and caudally. Margined mesally and also caudally and laterally, the lateral margin wide.

Anal scale roughly triangular, the anterior margin convex, the caudo-lateral sides very weakly convex, meeting at middle line in an acute angle.

Ventral plates with longitudinal and transverse sulci well developed.

Legs of moderate length; bristles densest distad; ultimate joint densely and subseriately setose ventrally.

First and second legs in male strongly reduced, the second pair a little larger than the first.

For structure of gonopods of male see Pl. X, fig. 3.

Length 19-20 mm.; width 2.2 mm.

Locality: Madison, Washington. (Dr. E. Bergroth).

## Family XYSTODESMIDÆ.

Genus *Xystocheir* Cook.*Xystocheir taibona* sp. nov.

Tegument thin, translucent, horn-brown in color, the carinal margins pale brick-red; prozonites paler; pigment about dorsal vessel commonly showing through as a dark median line. Head very light or whitish shining brown, a triangular dark spot below each antenna formed of closely arranged small dots. Antennæ light yellow or whitish. Legs pale yellow or yellowish brown, darker proximally. Venter and sides pale brown to yellowish.

A sharply impressed median sulcus crossing vertex and ending abruptly at about level of upper margins of antennal sockets or but little lower, crossing near its distal end a shallow furrow which arches across from the dorsal edge of one antennal socket to the other. Vertex smooth and shining. A few scattered bristles over frontal and clypeal region.

Antennæ rather long, uniform; clothed with rather short hairs intermixed with long bristles, especially on proximal segments.

First dorsal plate a little wider than the head, shorter than the second. Cephalic and lateral margins together semi-circular. Caudal margin mesally straight or very slightly incurved, laterally extending obliquely cephalad. Entire border margined. Two pairs of impressed lines, the two on each side diverging from near the mesal line caudo-laterad, the anterior one nearly straight, the posterior curved, its convexity caudo-mesad.

Second plate and those immediately following with lateral portions bent cephalad, farther back the plates becoming first straight and then with the lateral portions bent more and more caudad. In the anterior plates the cephalo-lateral portion bulges cephalad, but in proceeding caudad the anterior margin first becomes straight and then the antero-lateral corners more and more strongly rounded caudad, the posterior corners becoming at the same time more and more strongly produced. All scuta distinctly margined. Each segment crossed by two transverse sulci of which the more caudal is deepest and longer.

Nineteenth segment very short, the lateral processes ordinarily exceeded by those of the eighteenth segment.

Anal scutum with process a little depressed, truncate distally where it bears several groups long bristles, crossed with two rugose lines a double one at posterior third and the other midway between this and the apex of process, each line bearing two pairs of double setæ, two being inserted together in each case. In addition there is a marginal couple on each side of scutum farther cephalad.

Anal valves roughened; inner margins strongly elevated; each valve with two sulci extending from anterior margin caudad and somewhat laterad, the more mesal one with a double bristle inserted near its middle and each valve also bearing at its caudo-mesal angle a compact bunch of similar long setæ.

Anal scale with anterior margin incurved mesally and convex laterally, bow-shaped; each caudo-lateral margin convex, meeting its fellow of opposite side in a rounded obtuse angle. Scale crossed with a sulcus ending in the cephalo lateral corners and bending caudad across the plate; a weaker sulcus sub-parallel with this further cephalad; caudad of the first or principal sulcus and extending to caudad margin there is on each side of middle a longitudinal sulcus. Just ectad of the longitudinal sulcus on each side and nearly upon the caudal margin is a double bristle.

In the gonopods of the male the two rami on each side are fused excepting distally, the ventral one not separate and opposed to the other like a thumb as is the case in *F. dissecta* Wood. The principal or ventral ramus long and cylindrical, terminating in three spines which are inserted at the same level. Spines simply curved, not twisted; the ventral one flat, narrow, apically rounded; the outer one distally bent ecto-caudad, pointed; the dorsal one most slender. (See Pl. X, figs. 1 and 2).

Length ad 28 mm.; width 5 mm.

Locality: Region of Monterey Bay, Cal. (Pacific Grove, etc.)

A very common species in this locality (Author coll., 1902, 1909, 1911).

Related to *X. dissecta* (Wood) but the gonopods very distinct. *Xystocheir obtusa* Cook and *Fontaria furcifer* Karsch are doubtless synonyms of Wood's species. I have specimens of *dissecta* from near the type locality and find them to agree with Wood's description as well as with those of the two authors mentioned, when Woods' description is correctly apprehended. The nineteenth segment is somewhat variable in length, its distal processes occasionally extending considerably beyond those of the eighteenth, while in other cases the segment may be wholly covered by the eighteenth in which case the latter might be readily mistaken for the former.



## EXPLANATION OF PLATES.

## PLATE X.

*Xystocheir taibona* sp. nov.

- Fig. 1. Gonopods of male, caudo-ventral aspect.  
Fig. 2. The same, lateral aspect.

*Polydesmus bonikus* sp. nov.

- Fig. 3. Left gonopod of male, caudo-ventral aspect.

*Tilsona sima* gen. et. sp. nov.

- Fig. 4. Left leg of first pair, caudal aspect.

## Fig. 5. Antenna.

- Fig. 6. Head and anterior segments, lateral aspect.

*Buwatia monterea* gen. et sp. nov.

- Fig. 7. Antenna.

## PLATE XI.

*Paraiulus tivius* sp. nov.

- Fig. 1. Gonopods of male, caudo-ventral aspect.  
Fig. 2. Gonopods of male, lateral aspect.  
Fig. 3. Third pair of legs of male.  
Fig. 4. Second pair of legs of male, caudal aspect.  
Fig. 5. First pair of legs of male, caudal aspect.  
Fig. 6. Gnathochilarium of male.  
Fig. 7. Sensory hair from lateral region of clypeus.

*Paraiulus limpius* sp. nov.

- Fig. 8. Gnathochilarium of male.  
Fig. 9. Gonopods of male, lateral aspect.

## PLATE XII.

*Soniphilus geronimo* sp. nov.

- Fig. 1. Head, dorsal aspect.  
Fig. 2. Head and prehensorial feet, ventral aspect.  
Fig. 3. Caudal region of body, ventral aspect.

*Poabius nankus* sp. nov.

- Fig. 4. Right anal leg, dorsal aspect.

*Paraiulus garius* sp. nov.

- Fig. 5. Anal scale.  
Fig. 6. Caudal end of body, lateral aspect, showing anal valves, scutum, etc.  
Fig. 7. Same, dorsal view.  
Fig. 8. Appendages of second segment of female as seen from lateral and slightly cephalic view. First segment partly separated from the second.

## PLATE XIII.

*Poabius verdescens* Chamberlin.

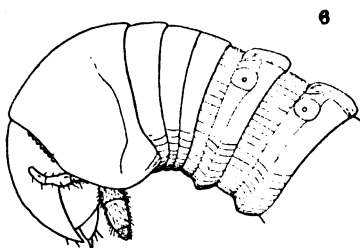
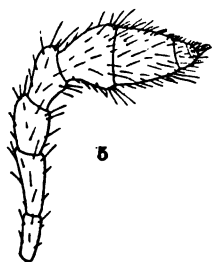
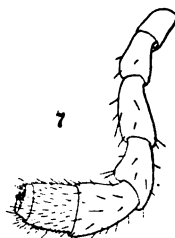
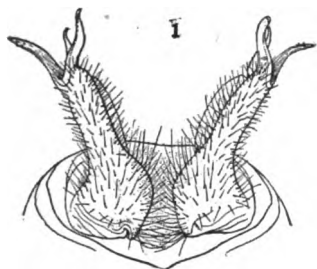
- Fig. 1. Right anal leg, dorsal aspect.

*Poabius iginus* sp. nov.

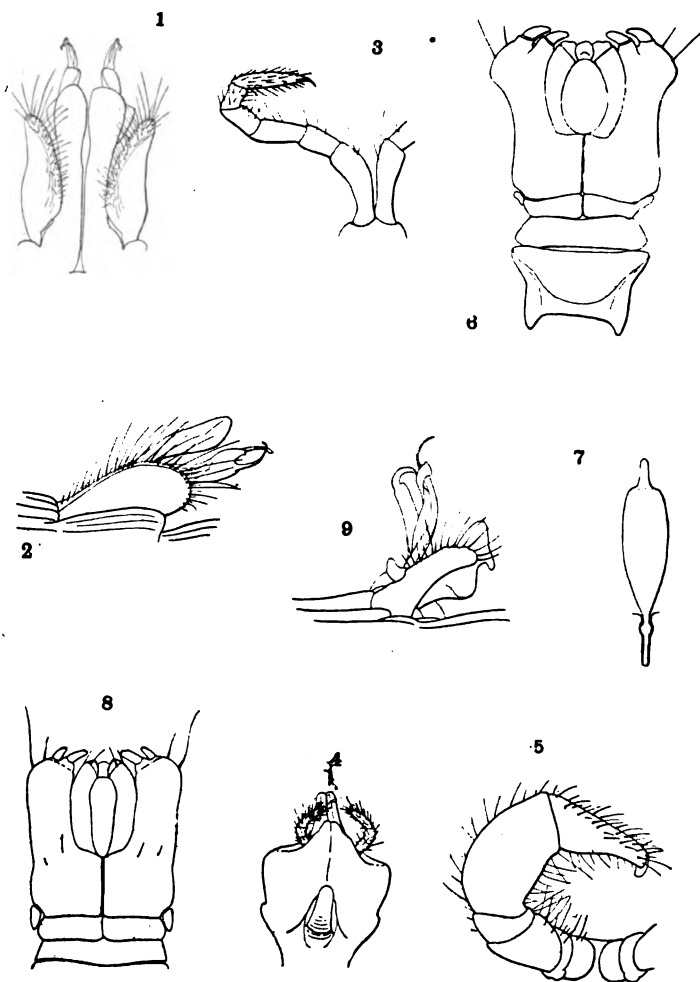
- Fig. 2. Right anal leg, dorsal aspect.

*Kethops utahensis* Chamb., gen. nov.

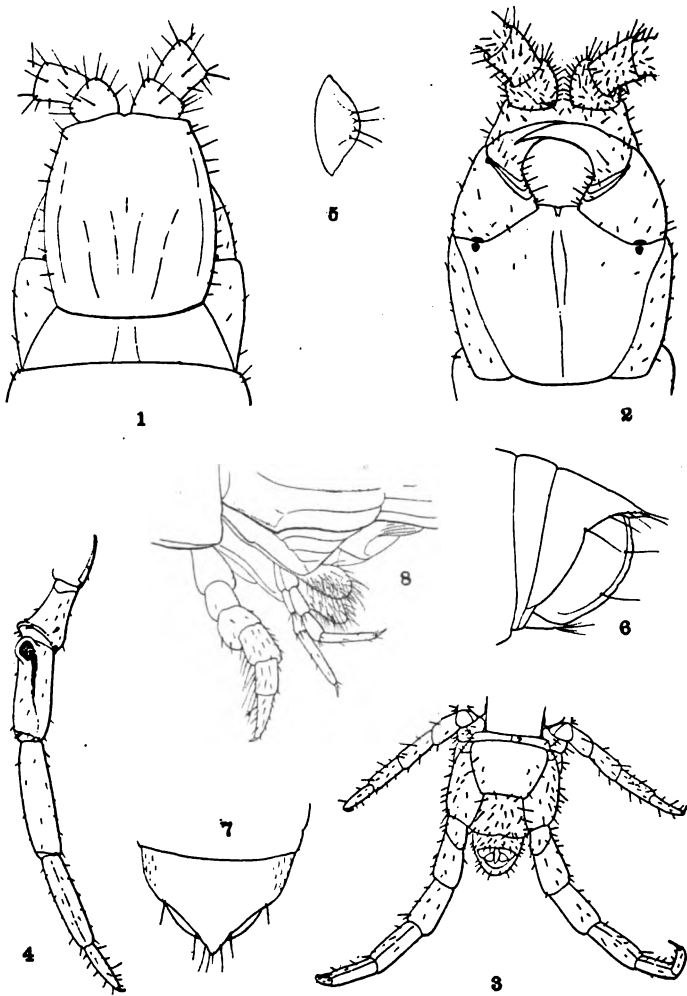
- Fig. 3. Last two segments, dorsal aspect.  
Fig. 4. Last segment, ventral aspect.  
Fig. 5. Fourteenth ventral plate.  
Fig. 6. Right anal leg, mesal aspect.



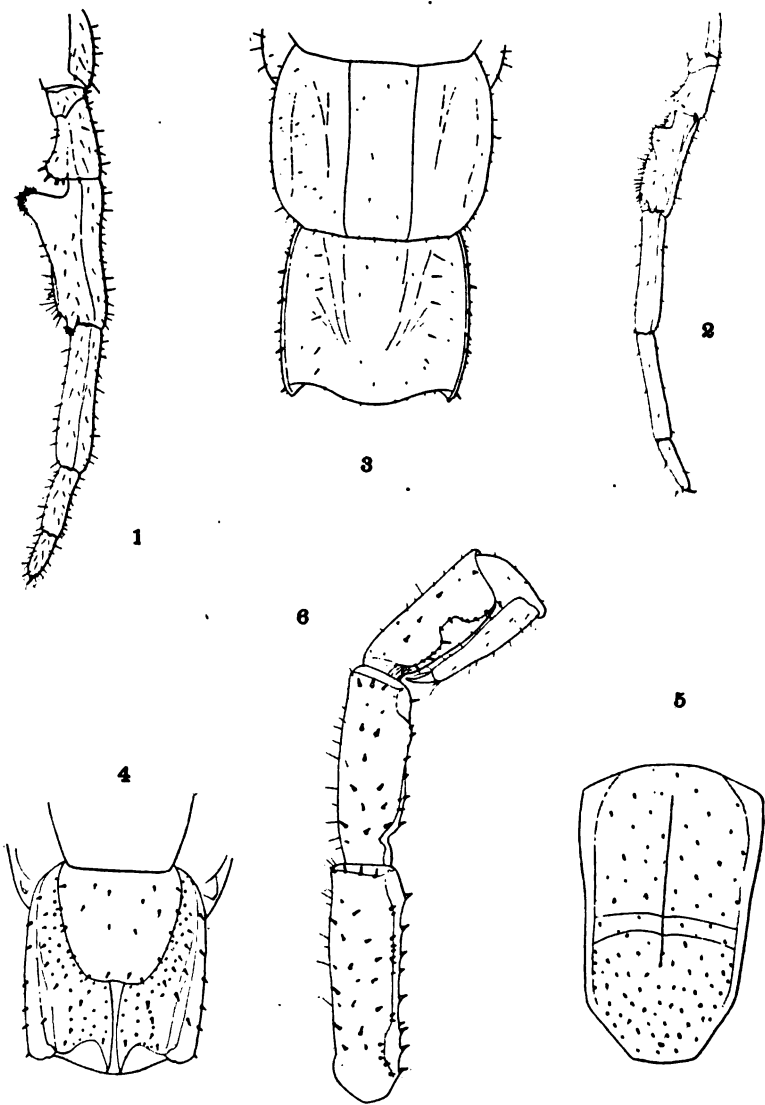
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**THE HENICOPIDAE OF AMERICA NORTH OF MEXICO.**

**BY RALPH V. CHAMBERLIN.**

**WITH FIVE PLATES.**

**CAMBRIDGE, MASS., U. S. A.:**

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No. 1.— *The Henicopidae of America north of Mexico.*

BY RALPH V. CHAMBERLIN.

THE genus *Henicops* was proposed by Newport in 1844 for two species, *H. maculatus*, from Van Diemen Land, and *H. emarginatus*, from New Zealand. Twenty-four years later Meinert described from Europe a species obviously related to these, placing it under a new genus as *Lamyctes fulvicornis*; but by common consent subsequent workers have, until recently, dropped *Lamyctes* as a synonym of *Henicops*. However, in 1901, Pocock restudied Newport's species and pointed out that *maculatus*, which he specified as the type of *Henicops*, differed from the European species in having the tarsi of the fourteenth and fifteenth pairs of legs, six segmented and those of the anterior pairs trisegmented, the last three pairs of legs in *fulvicornis* having the tarsi only bisegmented and the anterior legs having the tarsi wholly undivided. In accordance with these important differences Pocock again recognized *Lamyctes* as a distinct genus, at the same time describing two new genera evidently closely allied, *Haasiella* and *Paralamyctes*.<sup>1</sup> Other genera having more or less close affinities with *Henicops* and *Lamyctes* have also been described by Silvestri<sup>2</sup> and by the present writer. Silvestri and Pocock place these genera, which, it may be noted, occur in the main in the Southern Hemisphere, in a family *Henicopidae* in contrast particularly with the *Lithobiidae*, including *Lithobius* and allies which abound for the most part in the Northern Hemisphere; but Verhoeff in his recent revision of the *Lithobiomorpha* in *Die klassen und ordnungen des thierreichs* (1907, 5, p. 245f), does not recognize the family, denying the sufficiency of the basis for it. Careful study of the genera of the *Lithobiomorpha*, however, makes it very obvious that these (omitting those of the *Cermatobiidae*) fall into two compact and clearly separated groups and that, as one of these, the *Henicopidae* must be given recognition as a distinct and well-defined family.

<sup>1</sup> R. I. Pocock, Some new genera and species of lithobiomorphous chilopoda. *Ann. mag. nat. hist.*, 1901, ser. 7, 7, p. 448-451.

<sup>2</sup> F. Silvestri, Descrizioni di alcuni generi e specie di *Henicopidae*. *Boll. Lab. zool. R. scuola sup. agric. Portici*, 1910, 4, p. 38-50.



The following points in which the Lithobiidae differ from the Henicopidae may be mentioned as the most important thus far noted:—

1. The labrum is tridentate instead of unidentate.
2. The inner branch of the first maxillae is armed with ramose or plumose hairs.
3. The outer branch of the first maxillae is only biarticulate.
4. When present, the eyes consist of from several to many ocelli.
5. Sternite of prehensorial segment absent, never constituting a distinct transverse sclerite or collar.
6. On none of the legs is a true tibial process or spur ever present.
7. Articular spines are present on at least part of the legs cephalad of the fourteenth pair.
8. Anal pores never present in adults.
9. Gonopods of male composed of one or, at most, of two articles and never terminating in a pointed process or rudimentary claw.

In regard to point 7 it may be mentioned that in *Watobius* and allies (subfamily *Watobiinae mihi*), which differ from the typical Lithobiidae in other points also, spines are present only on the tibiae in the place occupied by the tibial spur in the Henicopidae; while in the Henicopidae spines may very rarely occur on trochanter or on trochanter and prefemur of the fourteenth and fifteenth pairs of legs.

The following definition of the Henicopidae is based primarily upon a study of the North American representatives.

#### **HENICOPIDAE** (*char. emend.*).

Labrum mesally deeply incised; unidentate; margins of lateral divisions bearing either plumose or else simple or nearly simple hairs.

Inner branch of first maxillae armed with simple hairs exclusively, or in part with hairs simply and shortly laciniate at tips. Outer branch triarticulate; clothed distally with plumose hairs.

Palpus of second maxillae triarticulate; claw four or five partite; distal article bearing on ventral surface toward distal end few to many plumose (ramose) hairs.

Eyes either entirely absent or consisting of a single large ocellus on each side.

Organ of Tömösvary large; situated on ventral border of head, typically caudad of position of ocellus.

Sternite of prehensorial segment well developed, extending trans-

versely as a narrow sclerite or "collar" caudad of the prosternum proper.

Tibia of all legs, or of all excepting the last one to three pairs, bearing at the distal end on the cephalic or cephalodorsal side an acute or spinous tipped process or spur. True articular spines either wholly absent (as in all N. Amer. species) or present only on last two pairs of legs.

Spiracles present on 3rd, 5th, 8th, 10th, 12th, and 14th segments, as in the Lithobiidae, or, in addition also on the 1st; or rarely present only on the 3rd and 10th segments (*Catanopsobius*).

Coxal pores present on the last two to five pairs of coxae.

Anal pores always present in adults and consisting of a single well-developed pair opening into a common median passage.

Gonopods of female long, triarticulate, and ending in a stout, strongly chitinized claw which is always entire; basal spines, so far as known, 2 + 2 or 2 + 3. 2nd article glabrous dorsally. Gonopods of male likewise long and triarticulate; ending in a straight, weakly chitinized process usually terminating in a bristle.

Three genera of this family are at present known to occur in America north of Mexico. They may be separated by means of the following key.

aa. A pair of spiracles on the first leg-bearing segment.

*Henicopinae* Chamb.

Tarsi of anterior legs undivided.

*Lamyctes* Meinert.

aa. No spiracles present on the first leg-bearing segment.

*Zygethobiinae* Chamb.

b. Ocelli absent; only the coxae of the last four pairs of legs bearing pores.

*Buethobius* Chamberlin.

bb. A pair of large ocelli present; coxae of last five pairs of legs bearing pores.

*Zygethobius* Chamberlin.

#### LAMYCTES Meinert.

Naturh. tidsskr., 1868, 5, p. 266.

Labrum of usual form; lateral pieces not notched each side of median tooth; sides bearing sparse and simple hairs. (Plate 1, fig. 6).

Inner branch of first maxillae bearing few and entirely simple hairs. Outer branch armed with simple and plumose hairs. (Plate 1, figs. 3 and 4).

Eyes present, each consisting of a single large ocellus.

Antennae short; articles 24 to 31, but mostly 25 or 28 (in *N. Amer.* forms); articles beyond the second short, with marked tendency for shortest ones to recur in pairs.

Prosternum conspicuously narrowed cephalad, with anterior margin narrow. Teeth 2+2 or 3+3. (Plate 1, fig. 7).

Seven pairs of spiracles present, one pair being present on the first leg-bearing segment.

None of the dorsal plates with posterior angles produced (in *N. Amer.* species).

First eleven or twelve pairs of legs with tarsi entire, bearing a tibial process (Plate 1, fig. 12); last three pairs with tarsi biarticulate and tibiae without processes. Coxae of last pair of legs without caudal processes.

Coxal pores present on last four pairs of legs.

TYPE.—*L. fulvicornis* Meinert.

The four species known from the United States are small forms less than 19 mm. long. Males of none of them have been found. The species of this genus are difficult to discriminate.

#### *Key to species.*

- a. Articles of antennae normally 25; first tarsal joint of anal legs only about four times as long as its greatest width.<sup>1</sup>  
*L. fulvicornis* Meinert.
- aa. Articles of antennae 28 (–31); first tarsal joint of anal legs eight times or more as long as its greatest width.
  - b. Length 5 to 6.5 mm. *L. tivius* Chamberlin.
  - bb. Length at least 7 mm.
    - c. Greatest thickness of femur of anal legs 1.5 times the greatest thickness of tibia; antennae 3.7+ times the length of head. *L. pinampus* Chamberlin.
    - cc. Greatest thickness of femur of anal legs but 1½ times greatest thickness of tibia; antennae 3.2± times the length of head. *L. pius* Chamberlin.

<sup>1</sup> In measuring the joints of the anal legs the method uniformly followed by the author has been to detach one leg and mount it with mesal surface down, measurements being then made by means of an ocular micrometer.

## LAMYCTES FULVICORNIS Meinert.

Naturh. Tidsskr., 1868, 5, p. 266.

*Lithobius gracilis* Porath, Öfvers. Kongl. vet. akad. forh., 1869, 26, p. 641.

*Lamyctes fulvicornis* Stuxberg, Öfvers. Kongl. vet. akad. forh., 1871, 28, no. 4, p. 504.

*Lamyctes fulvicornis* Meinert, Nat. tidsskr., 1872, 8, p. 343.

*Lamyctes fulvicornis* Stuxberg, Öfvers. Kongl. vet. akad. forh., 1875, 32, no. 2, p. 72.

*Lamyctes fulvicornis* Stuxberg, Proc. Cal. acad. sci., 1877, 7, p. 138.

*Henicops fulvicornis* Latzel, Die myriop. Oest.-Ung. monarchie, 1880, pt. 1, p. 133, pl. 4, figs. 31-34.

*Henicops fulvicornis* Haase, Schlesiens chilopoden, 1880, 1, p. 42.

*Henicops fulvicornis* Bollman, Entom. Americana, 1888, 4, p. 6.

*Henicops fulvicornis* Bollman, Bull. 46, U. S. N. M., 1893, p. 184.

*Henicops fulvicornis* Chamberlin (in part), Proc. U. S. N. M., 1902, 24, p. 797.

*Lamyctes fulvicornis* Chamberlin (ad part. max.), Ann. Ent. soc. America, 1909, 2, p. 191.

*Lamyctes fulvicornis* Chamberlin, Pomona college journ. ent., 1910, 2, p. 368, fig. 132 A.

*Lamyctes fulvicornis* Chamberlin, Can. entom., 1911, 43, p. 67, 98.

DIAGNOSIS.—Yellowish brown to chestnut, posterior segments and first one often darker; head mostly brownish red, often blackish along the suture; legs dusky yellow, posterior pairs brownish. Body slender, nearly eight times longer than width of tenth plate, from which the sides are nearly parallel cephalad. Head subcordate, equal in length and breadth or nearly so. Antennae short, the body being about 3.5 times longer; submoniliform; articles 25 (rarely 24 and 28 or 29). Prosternum cir. 1.75 times wider than long; teeth 3+3, the outer on each side smaller. None of dorsal plates with posterior angles produced. Coxal pores circular; usually 2, 3, 3, 3 or occasionally to 2, 4, 4, 4. Anal legs short, the body being cir. 3.5 times longer; tibia between 3 and 3.5 times as long as its thickness dorsoventrally; first tarsal joint 4 times as long as thick dorsoventrally. Gonopods of female with claw long and acute, curved; basal spines 2+2 or, rarely, 2+3, conical, with tips often bent. Length 7-11 mm., but mostly 7-9 mm.

**DESCRIPTION.**—Dorsum yellowish to chestnut brown, the posterior segments darker as is also frequently the first one. Head, together with the prehensors and prosternum, brownish red; the head frequently darker, blackish, along the frontal suture. Antennae yellowish red with the yellow sometimes dominating; mostly darker proximally than distally. Legs dusky yellow or brownish yellow, sometimes a little reddish distally; posterior pairs darker. Venter dusky brownish yellow with the posterior segments darker, brownish or, in some, of reddish caste.

Slender; but little attenuated cephalad from eighth segment; distinctly attenuated caudad from tenth segment as usual; 8 to 8.5 times longer than width of tenth plate. Body in general sparsely hairy, the hairs being more numerous on the legs; antennae densely clothed, the hairs more numerous distad.

Head subcordate; equal in length and breadth or very nearly so. Rugose; commonly two or three pairs of longitudinal furrows, one pair diverging cephalad with others on caudolateral portion. Punctae rather coarse and scattered.

Prosternum considerably produced cephalad, attaining the meso-distal end of prefemur; anterior edge narrow, at middle narrowly incurved. Teeth 3+3, of which the outer on each side is at the edge of anterior margin, commonly much smaller than others and spinescent (Plate 1, fig. 7). Prosternum not quite 1.75 times wider than its greatest length.

Antennae short, about 2.4 times longer than the head while the body is about 3.5 times their length. (In small specimens often relatively longer, ratio to body length being sometimes as much as 1:2.7). Submoniliform. Nearly always composed of 25 articles, very rarely of 28 or 29, or, in the other direction, of 24. First two articles long, the second being clearly the longer as usual; all others decidedly shorter; the tenth and eleventh articles uniformly shorter than the adjacent ones and in most the third and fourth articles also shortened, though frequently the fourth is shortened without the third as may also be the eleventh without the tenth.

Dorsal plates well arched; in adults mostly with a rather wide longitudinal furrow each side of the middle; the lower lateral and caudal borders set off by sulci paralleling the margins. Sometimes a very shallow median longitudinal furrow may be detected. First, third, fifth, eighth, tenth, twelfth, and fourteenth dorsal plates with caudal corners rounded and with a caudal margin mesally incurved. Seventh plate with caudal margin mesally straight, not at all incurved;

caudal corners rounded. Ninth and eleventh plates with caudal corners obliquely truncate or excised; caudal margin of thirteenth plate straight.

Ventral plates rugose and uneven; on most a deeper furrow parallel with and not far from the anterior margin and a similar one toward caudal margin, the two on anterior plates often united at ends by longitudinal furrows and thus forming a large rectangular impression.

Twelfth to fifteenth pairs of legs without tibial process. Tarsi of last three pairs of legs distinctly biarticulate; those of the immediately preceding legs often showing a suture faintly developed. All others with tarsi strictly undivided.

Anal legs short, about equalling the antennae, the body being thus near 3.5 times longer. Tibia mostly between 3 and 3.5 times as long as thickness dorsoventrally; first tarsal joint four times as long as dorsoventral thickness; the second tarsal joint 4.6 times longer than thick. Length of anal legs to that of the penult about as 4:3.

Coxal pores small, circular; mostly 2, 3, 3, 3, occasionally 2, 4, 4, 4. Each pore bearing coxa commonly with a longer bristle at distal ventral edge.

Gonopods of female sparsely pilose; claw long, acute, and entire, moderately bent and with concave side excavated; basal spines 2+2 (with rarely an extra one on one side), conical with one or both of each pair often bent ectad at tip.

Length 7-11 mm., but mostly 7-9 mm.

*Agenitalis*.— Very pale yellowish brown, with a violet tint showing through from the tissues beneath chitin; head yellowish with the region of eyes and apex of head darkened.

Ocellus very distinct.

Antennae composed of 21 to 23 articles.

Prosternal teeth 3+3, the outer one on each side minute.

Coxal pores 1, 1, 1, 1.

Gonopods extended but showing no trace either of claws or of basal spines.

Length 4.5-5 mm.; greatest width .6-.7 mm. (Latzel).

TYPE LOCALITY.— Europe.

NORTH AMERICAN LOCALITIES.— Maine (Orono!); Massachusetts (Cambridge!); New York (New York City at Mt. Lebanon!); Pennsylvania!; Wisconsin (Haugen! Eau Claire! Ashland! Beloit! Menominee!); Michigan (Powers! Watersmeet! Marinette!); Illinois (Peoria!); Minnesota (Winona!); Nebraska (Omaha!); Colorado (Colorado Springs!); Utah (Lake Point! Salt Lake City! East Mill

Creek! Provo!); Idaho (Pocatello!); Oregon (Portland!); Arkansas (Little Rock, sec Bollman, but possibly not the real *fulvicornis*).

Also distributed throughout Europe.

No male of this species has ever been recognized. The author has examined more than a hundred individuals without detecting a male and has sectioned a considerable number of females without finding spermatozoa in the genital ducts although these are to be found readily enough in female *Lithobii*. The present evidence lends probability to the view that this species, as likely also its relatives in North America, is parthenogenetic in its usual reproduction.

This species prefers the immediate vicinity of water although the author has found it well removed from streams at times. In Wisconsin it is very common among stones and sticks at edges of streams and it was found in similar localities at Peoria, Illinois. At times it may be seen to go beneath the water if the rock upon which it is running is partly submerged.

#### LAMYCTES TIVIVS Chamberlin.

Ann. Ent. soc. America, 1911, 4, p. 33.

DIAGNOSIS.—Yellowish brown to dark brown, the last segments and the first one mostly darker. Head dusky or blackish about eyes and along suture with frontal region commonly paler. Legs yellow to brown. Body slender; between eight and nine times longer than the width of tenth plate; narrowed gradually from eighth plate cephalad. Body nearly glabrous, the hairs being short and very sparse. Head subcordate, slightly longer than wide. Antennae short; submoniliform; articles 28, varying occasionally to 31. Prosternum cir. 1.68 times wider than long; teeth 3+3, the outer one each side small and spiniform. None of dorsal plates with caudal angles produced. Coxal pores small; 2, 3, 3, 3. Anal legs short; tibia 4.5 to 5.5 times longer than thick; first tarsal joint cir. 8 times (rarely to only 7 times) longer than thick. Length 5–6.5 mm.

DESCRIPTION.—Dorsum yellowish brown to very dark brown, with the anterior and posterior segments darker as usual, dusky in the darker individuals. Often a more or less irregular dusky median band showing especially on the more anterior and more posterior segments, the borders of which are also sometimes darker. Head blackish about eyes and along suture, with the frontal region often distinctly paler.

Prosternum and prehensorial feet also of about same shade as head. Legs and antennae yellow or, in darker individuals (see var. *a infra*), the latter brownish with distal end paler and the anal legs dusky. Venter greyish to yellowish brown, the posterior segments darker as usual.

Slender; the body attenuate gradually and but little from the eighth segment cephalad and more abruptly narrowed from the tenth segment caudad; from eight to nine times longer than width of tenth plate. Nearly glabrous, being provided very sparsely with very short hairs which are more numerous on the legs. Antennae densely clothed as usual.

Head subcordate; nearly equal in length and breadth being but slightly longer (ratio 35:33 or less). Marked with two diverging sulci on posterior portion and with a number of shorter and more indistinct ones more lateral much as in *fulvicornis*. A weak furrow extending from anterior edge between antennae caudad to suture and more indistinctly to caudal margin.

Prosternum relatively a little narrower than in *fulvicornis*, being usually but about 1.68 times wider than greatest length. Extending forward to same point, or nearly so, as in *fulvicornis*. Prosternal teeth, small; 3+3, the outermost on each side much the smallest, minute or rarely obsolete or absent.

Antennae short; cir. 3.2+ times longer than the head, while the body is nearly 2.8 times longer than them. Antennae distad of the large second article submoniliform, and the articles all short. Articles from 28, the most usual number, to 31; the third and fourth, seventh and eighth, and tenth and eleventh are nearly always conspicuously shorter than the adjacent articles, while in some individuals the thirteenth and fourteenth may also show reduction. (See Plate 2, fig. 10).

Dorsal plates with the median region strongly arched and the borders low with the edges somewhat uplifted as in *fulvicornis*, presenting a longitudinal sulcus parallel to lateral margin at inner edge of depressed border with a transverse sulcus parallel to caudal border and connecting the two lateral sulci, this transverse sulcus, especially on the more anterior major scuta sharply impressed and conspicuous. Convex portion of plate in front of the transverse suture with a weaker and finer longitudinal median sulcus and one or two pairs laterad of this. The transverse sulcus, especially on the anterior segments, seems to be much more distinct than in *fulvicornis* and also relatively farther from the caudal margin. Caudal margins of minor plates



straight, or that of ninth a little bent forwards at ends but the corners of none obliquely truncate.

Ventral plates commonly roughened by transverse furrows of which one toward the anterior edge and one toward the caudal are most distinct and of these two the caudal one commonly more deeply impressed.

Tibial processes and segmentation of tarsi as in *fulvicornis*.

Anal legs short; longer than antennae in ratio 12:11, longer than penult legs in ratio 3:2; body about 2.6 times longer. Tibia 4.5-5.5 times longer than thick; first tarsal joint 7-8 times longer than thick, mostly 8 times longer; second tarsal joint 7.5 times longer than thick. (See Plate 2, fig. 9).

Coxal pores small, circular, nearly always 2, 3, 3, 3.

Claw of female gonopods long, pointed, a little curved and concave mesally as usual. Basal spines 2+2, rather stout, conical, somewhat flattened distad and often bent ectad toward tips.

Length 5-6.5 mm.

*Agenitalis* — Stage I. — Body and head light brown, the latter dusky or blackish at sides. Antennae and legs very light, brownish white.

Ocellus distinct but pale.

Antennae composed of 24 articles; distad of second article strictly moniliform.

Prosternal teeth small and pale; 3+3, the outer one minute, the relations being the same as in the adult.

Dorsal plates showing the transverse furrow very distinctly, the lateral ones also being evident; the median elevated portion of plate with a median and, on each side of it, another distinct longitudinal sulcus.

Coxal pores 1, 1, 1, 1.

Anal glands very distinct.

Gonopods appearing as short conical buds, already three jointed, but with no trace of claw or basal spines and entirely lacking hairs.

Length 3.4 mm.

New Orleans, var. a.

*Pullus* — Stage IV. — Coloration nearly as in the *immaturus* but a little paler.

Ocellus pale.

Antennae in one specimen composed of 19 articles of which the eleventh, twelfth, thirteenth, and sixteenth show signs of subdivision. In a second specimen apparently slightly less advanced than the preceding, 15 articles are present in the right antenna, which seems to be regenerating after a loss, and 20 on the left. Beyond second article strictly moniliform.

Three last pairs of legs appearing as long, closely appressed buds, of which the first, in one specimen, is very faintly segmented distad of the coxa, the others more indistinctly so; pale; without trace of hairs excepting one long ventral bristle on the relatively large coxa of each leg.

A single coxal pore present on each coxa of twelfth legs, this a little pigmented.

Anal glands showing very distinctly.

Anal segment with a pair of short bristles immediately beneath glands and two pairs of very long setae caudad of the glands, the two bristles of each pair being near the median line and crossing each other obliquely.

Length cir. 3 mm.

New Orleans, var. a.

LOCALITIES.—Mississippi (Byram! Holly Springs!); Louisiana (New Orleans! var. a.); Alabama (Jackson!).

*Variety a.*—The specimens from New Orleans are uniformly darker than those from Mississippi and Alabama, appearing to be a little more strongly chitinized, the darker extremes of coloration noted in the description of the adults above being met with in these individuals. The tarsal and tibial joints of posterior legs are on the average also relatively more slender than in the others. Otherwise no differences could be detected, however, and complete intergradation is likely to be found.

NOTE.—The record of this species from Hot Springs, North Carolina, given in connection with the original description was an error, all specimens studied from that locality belonging to the next species. The measurement of 7.5 mm. given as the maximum length in the description mentioned pertained to a small specimen of the latter species, *L. pius*.

#### LAMYCTES PIUS Chamberlin.

*Lamyctes tivius pius* Chamberlin, Ann. ent. soc. America, 1911, 4, p. 33.

DIAGNOSIS.—Dorsum brown, the posterior segments darker and distinctly reddish. Head brownish red or chestnut, darkest back of suture. Legs yellowish, the more caudal ones darker and tinged with red. Body slender; cir. 8.8 times longer than width of tenth plate; less strongly narrowed cephalad than *tivius*. Head subcordate, slightly longer than wide. Antennae very short, being but one third

the length of the body; articles 28 (rarely 29). Prosternal teeth 3+3, the outer one reduced as usual. None of dorsal plates with posterior angles produced (for form see Plate 2, fig. 7). Coxal pores, 2, 3, 3, 3. Anal legs short, but longer than antennae, the body 2.6 times longer; tibia 5.7 or 5.8 times longer than thick dorsoventrally; first tarsal joint 8 to 9 times as long as thick; second tarsal joint 8 times longer than thick. Claw of female gonopods long, slender, and curved; spines rather stout, conical and distally flattened. Length 7.5-9.5 mm.

DESCRIPTION.—Dorsum brown, with the posterior segments darker and distinctly reddish. Head brownish red or chestnut, darker caudad of the frontal suture. Antennae light reddish brown, pale distad. Legs yellowish, the more caudal ones becoming brown and tinged, especially the proximal joints, with red. Venter brown, with the first and last segments darker; the prosternum and prehensors similar but tinged with reddish.

Slender, cir. 8.8 times longer than width of tenth plate; eighth and tenth plates of same width; body narrowed cephalad from eighth plate but little less than in *tivius*. Body sparsely clothed with short hairs which are as usual more abundant on legs; hairs of body rather more numerous than in related species, particularly than in *tivius*.

Head subcordate; very slightly longer than wide; roughened by a number of shallow longitudinal furrows.

Prosternum of nearly same form as in *fulvicornis*. Teeth 3+3, the outermost reduced as usual.

Antennae short; 3.2 times longer than head; one third the length of body; composed of 28 or rarely of 29 articles, of which those distad of the long second one are short and moniliform as in the other species; the third and fourth (or sometimes the fourth alone), seventh and eighth, tenth and eleventh, and thirteenth and fourteenth are reduced as in *tivius*.

Dorsal acute mostly with a pair of longitudinal furrows each side of middle which often rises ridge-like between them; in addition other smaller and more shallow, irregular furrows or sulci may be detected; furrows limiting the lateral and caudal depressed borders as in related species. Caudal margin of ninth and eleventh plates bowed forwards at ends, the corners of these plates in some appearing obliquely truncate but the line of truncation making but a slight angle with mesal portion of margin; caudal margin of thirteenth plate straight all the way across.

Ventral plates rugose; a deeper transverse furrow toward caudal

margin and one or two weaker ones parallel with this on anterior portion; a number of longitudinal impressed lines near sides.

Tarsi of last three pairs of legs biarticulate in the usual way, those of more anterior pairs undivided. Tibial process well developed on the first eleven pairs of legs and also weakly developed on the twelfth.

Anal legs longer than antennae in about ratio 15:13; longer than penult legs in ratio 5:3; tibia 5.7–5.8 times longer than its greatest, dorsoventral, thickness; first tarsal joint 8 to 9 times as long as thickness; second tarsal joint also about 8 times longer than thickness.

Coxal pores small and circular as in the other species; 2, 3, 3, 3.

Gonopods of the female with the claw long and rather slender; curved and excavated on mesal side; basal spines 2+2, rather stout, conical and somewhat flattened distad, the inner smaller than the outer.

Length 7.5–9.5. mm.

LOCALITIES.— North Carolina (Hot Springs! Asheville!); Georgia (Atlanta!); New Jersey (Westfield! Haddonfield!); Pennsylvania (Philadelphia!).

This species, it may be seen, in general structure and relative proportions parallels the preceding species, *L. tivius*, in a very close and interesting way; but it is at once to be distinguished by its conspicuously and constantly larger size and by its more reddish color. It also is less strongly narrowed cephalad, has some dorsal plates of somewhat different shape as above indicated, is more hairy and especially seems always to have the tibial and tarsal joints of the anal legs more slender. It seems also to occupy a distinct area, the center of which is probably the higher section of North Carolina and the adjacent parts of neighboring states; while *L. tivius* apparently occurs only in the lower and coastal region of the southeastern States.

#### LAMYCTES PINAMPUS Chamberlin.

Pomona college journ. ent., 1910, p. 2, 368, fig. 132 B.

*Lamyctes fulvicornis* Chamberlin (in part), Ann. Ent. soc. America, 1909, 2, p. 191.

*Lamyctes pinampus* Chamberlin, Ann. Ent. soc. America, 1911, 4, pl. 3, fig. 3.

DIAGNOSIS.— Dorsum dark brown, the caudal segments and often the first one darker; head brown to reddish brown, darker on sides about and in front of ocelli; legs dusky yellow to brown. Head sub-

cordate; slightly longer than wide. Body slender; near 8.25 times longer than width of tenth plate; sides but slightly converging cephalad. Antennae short; the body 2.5 times longer; articles 28, with third and fourth, seventh and eighth, tenth and eleventh, thirteenth and fourteenth, and sixteenth and seventeenth reduced. Prosternal teeth 3+3, of usual relative size and form. None of dorsal plates with posterior angles produced (for precise form see Plate 2, fig. 4). Coxal pores 2, 2, 2, 2 to 3, 3, 3, 3. Anal legs longer than in related species and much more so than in *fulvicornis*; body but about 2.35 times longer; tibia about 5.3 times longer than thick; first tarsal joint 8 times as long as thick. Claw of female gonopods nearly straight in adults, less curved than in the other species; outer spine robust, with the inner considerably smaller. Length 7-9 mm.

DESCRIPTION.—Dorsum dark brown, with the caudal plates and sometimes the first one darker; plates often darkened along middle and edges. Head darker, brown to reddish brown; darker on sides about and in front of ocelli. Antennae reddish yellow to yellowish red, the first two to four articles often distinctly less red than the others. Ventral plates dusky yellowish brown to brownish yellow, the caudal ones of reddish tinge. Legs similar in color to venter, uniform.

Slender; only very slightly narrowed cephalad from eighth plate; body nearly 8.25 or 8.3 times longer than width of eight and tenth plates, which are of same width.

Head subcordate; very slightly longer than wide. A shallow longitudinal furrow extending caudad between antennae; on posterior portion of plate two longitudinal sulci diverging cephalad and on each side of these chiefly two others which are shorter and extend mesocephalad; two weak transverse sulci a little in front of caudal margin; lateral borders often set off by weak, fine furrows parallel with margins.

Prosternum and prosternal teeth as in the preceding species or very nearly so; that is, both scarcely differing from that of the type species, *L. fulvicornis*, which see.

Antennae short; about 3.8 times longer than head; body about 2.5 times longer than antennae. Articles nearly always 28; of these the third and fourth (or fourth alone), seventh and eighth, tenth and eleventh, thirteenth and fourteenth, and sixteenth and seventeenth are typically more shortened than the others, though in a minor number the two latter are not different in length from the adjacent ones.

Dorsal plates with caudal and lateral furrows setting off a wide low border as in the other species. Elevated median portion with a

longitudinal median sulcus and, on each side of this, two or three sulci a little diverging cephalad. Form of ninth and eleventh plates varying with age and stage of chitinization; in larger, fully chitinized individuals the caudal margin is straight with the corners not excised, or occasionally shortly so on one side; in small individuals, on the contrary, the corners are usually more obliquely and more clearly excised, much as in *fulvicornis*; while intermediate specimens have the eleventh straight like the thirteenth, the ninth still retaining the obliquely truncate or excised corners. (Plate 2, fig. 4).

Ventral plates roughened with rather fine transverse furrows or sulci of which one or two toward the caudal margin are deeper. On most plates a fine longitudinal furrow parallel with each lateral margin. Usually last three or four plates marked on each side with several distinct furrows running obliquely from the edge mesocephalad; last segment finely roughened but lacking the transverse sulci except commonly the deeper caudal one.

Anal legs longer than in the other species, the length of body being only about 2.35 times greater; longer than penult legs in ratio 53:33, or about 1.6 times longer. Tibia 5.3 times as long as thick; first tarsal joint eight times as long as thick; and the second tarsal joint  $8\frac{1}{2}$  times longer than thick. Greatest thickness of femur to greatest thickness of tibia as 1.5:1. Thickness of tibia to that of first tarsal as 1.74:1. Lengths of third, fourth, fifth, sixth, and seventh articles to each other as 37:40:46:40:30.

Coxal pores small and circular; 2, 2, 2, 2 to 3, 3, 3, 3, but most often 2, 3, 3, 2,

Claw of gonopods in fully grown females nearly straight, less curved than in the other species; flattened or excavated on mesal side; more curved in younger specimens. Basal spines 2+2; conical; the outer on each side robust, the inner being relatively smaller than in the other species and usually more acute than the outer.

Length 7-9 mm. in types; will probably be found to range considerably above this.

*Praematurus*.—Living specimens secured at Las Vegas, Nev., were light brown with a marked violet tinge, the latter fading in alcohol. Head a little darker and weakly reddish. Antennae (alcoholic specimens) yellowish brown; more greyish, less pigmented, proximally. Legs pale. A specimen from Claremont, Cal., has dorsum light brown, with the first and last plates darker, especially along the caudal borders; head dark caudad of frontal suture and blackish on sides about ocelli which have a decidedly bluish cast, and the frontal region orange

and contrasting sharply with the remaining portion; antennae orange-brown, paler proximally and on distal article; venter dusky yellowish brown, the caudal segments tending to reddish.

Head of same form as in adult.

Dorsal plates as in small adults or nearly so; the ninth and eleventh plates obliquely excised much as in the adult *fulvicornis*, but the oblique line relatively shorter.

Prosternal teeth 3+3, small, pale, with the outer on each side minute; proportions of prosternum as in the adult.

Antennae composed of 26 to 28, but mostly of 27, articles; in a minor number of specimens subdivision of one or of two of these articles is weakly indicated.

Coxal pores 2, 2, 2, 2.

Gonopods nearly as in adult; claw a little more curved; basal spines stout, conical, the outer proportionately wider at base than in adult, the inner relatively more slender than in adult but not so much shorter as usual in this stage in *Lithobii*. Bristles nearly fully developed.

Length 6-6.5 mm.

LOCALITIES:— Nevada (Las Vegas!); California (Claremont!).

#### BUETHOBIVS Chamberlin.

Ann. Ent. soc. America, 1911, 4, p. 34.

Labrum deeply incised as usual at middle; tooth conical and strongly chitinated; lateral divisions with border each side of the incision bent abruptly dorsad, strongly chitinated, and weakly notched at mesocaudal angle in such a way as to leave there a small and at times nearly obscure blunt tooth-like process apparently homologous with the lateral tooth in *Lithobius*, etc.; edge of lateral divisions bearing long plumose hairs of which those at the mesal end of the series are distally lacinate and are longest and also bearing simple hairs in an area each side of the mesal incision. (Plate 3, fig. 6).

Mandibles bearing four dentate divisions of plate of which the one at end opposite the aciculi is simple and conical the other three being set obliquely and each tridentate with the middle tooth longest and the one toward convex surface smallest (see Plate 3, fig. 3); bearing at caudal corner of distal end a row of ten to twelve large, flattened, acute aciculi which are bipectinate over the distal portion and also ectad of these and the teeth a series of finer plumose bristles.

Outer branch of first maxillae rather indistinctly triarticulate; its ultimate article clothed on mesal surface with plumose bristles and bearing at anterior end a much larger lacinate bristle (see Plate 3, figs. 2 and 4). Inner branch small, discrete from coxa, clothed with simple bristles of which one at apex is upon a much broader base and is stouter than the others (see fig. 2).

Eyes absent.

Antennae of medium length or long. First two articles long, the immediately succeeding ten or eleven greatly shortened, with those more distad longer. Articles so far as known, 36 to 45.

Prosternum with the anterior margin wide, not narrowly produced as in *Lamyctes*; teeth small, mostly 3+3.

Six pairs of spiracles present, none occurring on the first leg-bearing segment.

None of dorsal plates, so far as known, with posterior angles produced.

First twelve or thirteen pairs of legs with an acutely pointed tibial process or spur; the tarsi of these legs only indistinctly or not at all divided, the suture not affecting the dorsal side of article, but in part detectable on ventral side. (Plate 3, fig. 9).

Coxal pores present on last four pairs of legs; pores few, uniseriate and small.

Both males and females occurring commonly under the same conditions.

TYPE.—*B. oabitus* Chamberlin.

In the known species the body is more slender than in *Lamyctes* and the legs are relatively longer. The coloration is light throughout, yellow and pale orange with no darker pigment occurring.

In addition to the type species one other is at present known. The two species may be discriminated as follows:—

#### *Key to species.*

- a. Antennae composed of 36 articles; more than half as long as the body. *B. oabitus* Chamberlin.
- aa. Antennae composed of 43–45 articles; nearly always clearly less than half as long as the body. *B. coniugans* Chamberlin.



**BUETHOBIVS OABIVS Chamberlin.**

Ann. Ent. soc. America, 1911, 4, p. 34.

**DIAGNOSIS.**—Dorsum, with antennae and legs, yellow; head and posterior plates of dorsum orange. Slender, being  $8\frac{3}{4}$  or more times as long as width of tenth plate; sides nearly parallel cephalad of tenth plate. Head broadly subcordate; wider than long. Antennae long, being more than half the length of the body; articles 30. Prosternum a little less than twice as wide as long; teeth small and pale, 3+3. Posterior angles of none of the dorsal plates produced. Legs long, the ultimate pair especially so, slender and without special lobes in the male; claw of anal and of penult legs single. Coxal pores small, circular. Claw of female gonopods long and slender; strongly curved; basal spines acutely conical, with the slender distal portion black. Gonopods of male long, attenuated distad; distal article bearing an acutely pointed spine. Length 10–12 mm.

**DESCRIPTION.**—Color in general yellow or light yellowish brown. The head, prosternum, and prehensorial feet, and, usually the more caudal segments both above and beneath, clear orange. Antennae and legs clear yellow.

Slender, the length being  $8\frac{3}{4}$  or more times as great as the width of the tenth dorsal plate. Nearly parallel sided for most of the length, being but little narrowed cephalad of the tenth plate, but more decidedly caudad as usual. Body in general sparsely hirsute; the dorsal plates with stouter bristles along the lateral margins and the minor ones with a transverse series near caudal margin; legs more densely clothed with finer hairs among coarser spinescent bristles which are few on tarsi, where they occur chiefly at the indicated juncture of first and second joints but more numerous on tibia and more proximal joints.

Head broadly subcordate; wider than long in about ratio 11:10; conspicuously narrowed in front of middle, caudad of which the sides but slightly converge; the caudolateral corners well rounded. (Plate 3, fig. 7).

Prosternum not much less than twice as wide as greatest length (32:17); not much produced cephalad, the anterior margin being very wide, widely angularly and but shallowly incised at middle. Teeth small, pale, 3+3, subequal; the innermost on each side well removed from the middle line; the middle tooth on each side farther from the outermost than from the innermost. (Plate 3, fig. 1).

Antennae long; clearly more than half the length of the body, ordinarily reaching the ninth segment. Articles 36; of which the first two are longest and the third shortest, the others increasing gradually from the third distad and commonly showing a tendency for single longer articles to alternate with pairs of somewhat shorter ones. Subdensely clothed with long bristles.

Organ of Tömösvary rather large, circular; on ventral border of head immediately in front of level of greatest width. (Plate 4, fig. 1).

Major dorsal scuta, excepting the sixth, with the caudal margin convexly rounding at corners and mesally weakly incurved; caudal margin of sixth plate slightly convex a little bent cephalad toward ends. Minor scuta have the caudal margin straight; the caudal corners of the second, fourth and sixth very shortly obliquely excised, at least on one side; the caudal margin of the ninth and eleventh, especially of the former, bent forwards at ends nearly always more strongly on one side than on the other, or else on one side only; caudal margin of thirteenth a little incurved mesally. Tergites well arched; marked with several pairs of somewhat irregular longitudinal sulci of which one a little each side of middle and mostly curving ectad at its middle and one or two each side farther toward the lateral margin are most constant and most sharply impressed; shorter impressions elsewhere largely breaking the surface into short and irregular fine rugae.

Most ventral plates with a distinct and rather wide transverse depression or furrow at level of legs, this furrow on some anterior segments replaced by two which are often considerably separated; usually several other transverse furrows or sulci which are more distinct on caudal portion of plate.

Legs all long, the ultimate pair being especially long and slender; anal and penult legs ending in a single claw or the accessory of the latter obsolete, all other legs terminating in three claws. (Plate 3, figs. 8 and 9).

Coxal pores small and circular; 3, 3, 3, 3-4, 4, 4, 4.

Gonopods of the female with the claw long, slender, and acute; strongly bent. Basal spines 2+2, acutely conical; the slender distal portion usually blackish. (Plate 3, fig. 10).

Gonopods of the male long; attenuated from base distad. Distal article ending in an acutely pointed spine. Genital duct opening through a distinctly protruding, broadly rounded process.

Length 10-12 mm. Width of tenth plate 1.3-1.4 mm.

LOCALITIES.—Mississippi (Byram! Canton!).

## BUETHOBIOUS CONIUGANS Chamberlin.

Can. entom., 1911, 43, p. 383.

**DIAGNOSIS.**—Light orange, with head and caudal segments darker; antennae and legs yellow, except anal pair of latter which are orange. Slender;  $8\frac{1}{2}$  times longer than width of tenth plate; only slightly narrowed cephalad. Antennae normally less than half the length of the body; articles 43–45; hairs shorter than in *oobitus*. Prosternum twice as wide as long; teeth 3+3, small. Legs all long and slender. Anal legs slender and about half the length of body. First thirteen pairs of legs with tibial process. Coxal pores 2, 2, 3, 2–3, 3, 3, 3. Gonopods of male well clothed with long bristles; ultimate article terminating in a straight spine which may be a little bent at end. Gonopods of female with claw long and acutely pointed and strongly curved; spines conical, flattened distad. Length 8–10 mm.

**DESCRIPTION.**—Light orange with caudal segments darker. Head also darker but with the frontal region pale. Antennae and legs yellow, darker proximally; caudal pairs of legs darker, orange, especially proximally.

Body slender, being about  $8\frac{1}{2}$  times longer than width of tenth plate; only little narrowed cephalad. Entire body sparsely clothed with short among longer coarser hairs; more densely clothed as usual on legs where the longer coarse bristles are more abundant on ventral surface of tibia and proximal joints than on the dorsal surface; hairs on tarsi shorter, a pair of coarse ones on ventral surface marking the junction of the two more or less consolidated articles with often a pair distad of this. (See Plate 4, fig. 3).

Head subcordate; widest near middle, caudad of where the sides are nearly straight and a little converging, while cephalad the head is strongly narrowed; caudal margin a little excurved. Wider than long in about ratio 40:39.

Prosternum twice as wide as long. Anterior margin wide, not much extended cephalad; angularly incised at middle. Teeth 3+3, small, subequal, the outer farther from the middle one than the latter from the most mesal.

Organ of Tömösvary large, circular, and colorless; on ventral border of head at level of greatest width.

Antennae nearly always considerably less than half the length of the body, the average ratio of length of body to that of antennae being near 2.45:1, the limits observed being 2 and 3 respectively to 1, the

greater length being the rarer. Subdensely clothed with hairs that are shorter than those of *oobitus*. Articles 43-45 of which the first two are largest, a succeeding series of about ten typically greatly shortened, those at the ends of the series being shortest, while the articles distad of this series become clearly longer.

Major dorsal plates, excepting the sixth, with the caudal margin a little convex and rounded at ends and mesally incurved; the sixth with corners obliquely excised with the intervening caudal margin straight or slightly excurved. Caudal margin of minor tergites straight, the corners of ninth and eleventh in most obliquely excised though in some distinctly excised on one side only while in others the ends of the caudal margin are merely more or less evenly curved forwards. Dorsal plates with mostly four distinct longitudinal sulci, one a little removed from each lateral margin and one a little each side of the median line, shorter broken impressed lines wrinkling the surface between them; a weaker transverse impression in front of caudal margin.

Ventral plates finely wrinkled transversely, mostly so on the caudal half to two thirds of length, and a longitudinal furrow or impression a little mesad from each lateral margin. Last two or three sternites smoother; often with fine impressed lines running from caudolateral edge cephalomesad but these short and not affecting the middle portion of plate.

Legs all long. First twelve pairs with tarsi undivided but with the tegument between the two parts not strongly chitinized and thus more or less flexible, there being, however, no true joints. Tarsi of last three pairs of legs truly biarticulate. First thirteen pairs of legs with spinous tipped process or spur. First thirteen pairs of legs with three well-developed claws; the fourteenth pair also with accessory claws but these reduced.

Anal legs long and slender and otherwise alike in both sexes; nearly half as long as body (7:15); longer than penult in about ratio 14:11.

Coxal pores circular and rather small; 2, 2, 3, 2-3, 3, 3, 3; the more proximal in each series smaller than the more distal.

Caudal process of 15th coxae long, acute, and spinous tipped.

Gonopods of male with the three articles all well clothed with long bristles. Terminal spine often a little bent at apex. Penial process cylindrical or more or less narrowed or constricted proximally. (Plate 4, fig. 3).

Gonopods of female with articles bearing long bristles ventrally, but glabrous on dorsal surface. Claw long and acutely pointed and

strongly curved. Spines 2+2, conical, flattened distad, the outer one on each side a little stouter.

Length of male 9-10 mm. Length of female 8-9 mm., the average size being less than that of male.

*Pseudomaturus*.— Body brownish yellow, with the head and caudal segments light orange; antennae and legs yellow.

Proportions in general nearly as in adult; but in specimen measured head a little longer than wide (47:46).

Antennae of about same proportionate length as in adults; composed of 39 articles in which the series of ten shortened articles following the second is already present.

Prosternal teeth 3+3 with relations as in *maturus*.

The long bristles of dorsum arranged chiefly along lateral edges and in a transverse row across caudal portion of each minor tergite and of sixth with a few in a transverse row across anterior portion; on ventral plates chiefly confined to a transverse row across anterior border; the hairs elsewhere short.

Coxal pores 2, 3, 3, 3; pigmented.

Tibial process of first thirteen pairs of legs distinct; no indication of subdivision in tarsi of first twelve pairs; claws as in *maturus*.

Anal glands strongly developed.

Sternite of genital segment with 8-10 bristles on each side. First and second joints of female gonopods each with about four, the third with 2-3 bristles. Claw of gonopods shorter and paler than in adults and more obtuse, well excavated on mesal side. Basal spines smaller than in adult but nearly similarly related, but the inner ones relatively a little smaller.

Length 7.5 mm.

*Praematurus*.— Coloration nearly as given for *pseudomaturus*.

Head a little longer than wide.

Dorsum with relatively very long setae along the lateral margins of plates, the one at each posterior corner directed caudad. Each minor tergite with the usual transverse row of bristles along caudal border. Fewer long bristles in a transverse row across anterior border of each ventral plate.

Antennae relatively shorter than in adult and *pseudomaturus*. Articles 31 with the series of more shortened ones succeeding the second consisting of but 5, each of which probably would normally divided give to the series the adult number.

Prosternal teeth 3+3; small and pale; related as in *maturus*.

Coxal pores 1, 2, 2, 2.

Anal glands well developed.

Sternite of genital segment bearing on each side three bristles. First article of female gonopods with three bristles, second with two or three and the ultimate with two of which one is long and one short. Claw pale and thin, weak. Basal spines all present, but short and pale with the inner one of each pair more slender and much shorter than the outer, extending scarcely distad of the middle of the latter.

Length 6.75 mm.

LOCALITIES:— California (Berkeley! Mill Valley!).

### ZYGETHOBIUS Chamberlin.

Ent. news, 1903, 14, p. 335.

Labrum mesally deeply incised and unidentate as in other genera of the family; tooth acutely conical and strongly chitinized; lateral divisions not at all notched at median excavation. Lateral portions with a fringe of plumose hairs along margin much as in *Buethobius*, some of which also occur on caudal portion of dorsal surface which also bears more cephalad an area of simple hairs (see Plate 5, fig. 2).

In the mandibles at distal end and beginning at cephaloventral end of dentate plate are, first, three pairs of stout, obliquely placed teeth followed next to caudal angle by a fourth pair consisting of one large tooth and a much smaller one. Pectinate aciculi and plumose hairs nearly as in *Buethobius* but the aciculi fewer, being mostly about 6 in number (see Plate 5, fig. 5).

Both branches of the first maxillae separated from the coxae. Inner branch armed with simple hairs and hairs that are laciniate at distal end, the latter showing two, three, and more branches, but no truly ramose or plumose hairs are present. Outer branch clearly triarticulate; the ultimate article bearing plumose hairs on mesal surface; no branched aciculi at anterior end. (Plate 5, figs. 3 and 4).

Eyes present, each consisting of a single large ocellus which is larger than that in *Lamyctes* and is situated farther forward.

Antennae long; in known species consisting of from 38 to 43 articles.

Prosternum with anterior margin wide and not much extended forward; teeth 3+3. (Plate 4, fig. 6).

Only six pairs of spiracles present, none being found on first leg-bearing segment.

Posterior angles of ninth, eleventh, and thirteenth, or of these with seventh, or of these with both sixth and seventh, strongly produced.

First fourteen pairs of legs or else all fifteen pairs with acute tibial process. (Plate 4, fig. 8). Prefemur of legs with small pointed process at distal end on dorsal side. Tarsi of all legs biarticulate. The first tarsal joint increasing in size from first to last pairs of legs, in the caudal pairs being very long and slender. All legs ending in three claws.

Coxal pores present on the last five pairs of legs.

Both males and females occurring commonly under the same conditions.

Gonopods of female of type usual in family, the claw being large and entire and serrate along dorsal edge (see Plate 4, fig. 4).

Gonopods of male with ultimate article ending in a large, straight, weakly chitinated process or claw the edges of which are finely serrate (see Plate 5, fig. 8).

TYPE.—*Z. dolichopus* Chamberlin.

The members of this genus are of medium size. The body in all is conspicuously narrowed cephalad from the eighth segment and the legs are relatively long, particularly the posterior pairs. Of the four species at present known, three occur in the mountains of the western part of the continent, the fourth occurring in the mountains of Virginia and Tennessee.

#### *Key to subgenera and species.*

- a. First fourteen pairs of legs with tibial spurs, none being present on the anal pair; posterior angles of ninth, eleventh, and thirteenth or of these and the seventh as well, produced.

*Zygethobius* Chamb.

- b. Body prevailing brown, reddish pigment being absent or nearly so; more loosely joined and relatively longer articles of antennae beginning with the fifteenth.

- c. Posterior angles of ninth, eleventh, and thirteenth dorsal plates produced; articles of antennae 39 or 40; body eight times longer than width of tenth dorsal plate.

*Z. dolichopus* Chamberlin.

- cc. Posterior angles of seventh, ninth, eleventh, and thirteenth dorsal plates produced; articles of antennae 41; body but about seven times as long as width of tenth plate.

*Z. columbiensis*, sp. nov.

- bb. Body brown to chestnut, reddish pigment commonly promi-

nent; more loosely joined and relatively longer articles of antennae beginning with the seventeenth.

Body eight times as long as width of tenth plate.

*Z. sokarienus* Chamberlin.

- aa. All legs with well-developed tibial processes; posterior angles of sixth, seventh, ninth, eleventh, and thirteenth dorsal plates produced.

*Zantethobius* Chamb.

Articles of antennae 43; body seven times longer than width of tenth dorsal plate.

*Z. pontis* Chamberlin.

#### ZYGETHOBIUS DOLICHOPUS Chamberlin.

*Henicops dolichopus* Chamberlin, Proc. U. S. N. M., 1901, 24, p. 797.

*Henicops fulvicornis* Chamberlin, (in part), Proc. U. S. N. M., 1901, 24, p. 25.

*Zygethobius dolichopus* Chamberlin, Ent. news, 1903, 14, p. 335.

*Zygethobius dolichopus* Chamberlin, Pomona college journ. ent., 1910, 2, p. 368.

DIAGNOSIS.—Dorsum yellowish brown to dark brown, with first and last plates commonly darker and more reddish; head darker, often chestnut to nearly black with median and posterior portions paler; legs yellow to brown, more reddish distad, the posterior pairs darkest; the whole often suffused with violaceous. Head subrotund, longer than wide. Body strongly narrowed cephalad from tenth dorsal plate and more abruptly caudad; eight times longer than width of tenth plate. Antennae long; articles 39 or 40; articles distad of the fourteenth more loosely joined and showing an alternation of shorter ones in pairs with single longer ones, but the last six all long. Prosternal teeth, 3+3, small, the two innermost on each side closer together. Posterior angles of ninth, eleventh, and thirteenth dorsal plates produced. Coxal pores 3, 3, 3, 3-3, 4, 5, 5, 4, circular. Legs all long, especially the caudal pairs; tibial process present on legs of first fourteen pairs. Claw of female gonopods large, not strongly curved; basal spines 2+2 or 2+3; conical in outline, dorsally excised distad, with plane of inner nearly at right angles to outer. Length 11.4-12.6.

DESCRIPTION.—Color of dorsum yellowish brown to dark brown, first and last plates darker, sometimes reddish brown. Head frequently very dark, its anterior and lateral portions reddish, at times verging to black with the middle and posterior portions paler. Antennae yellow to brown, reddish brown or chestnut at base. Ventral plates smoky yellow. Legs mostly yellow, brown or somewhat red-



dish brown toward extremities; posterior pairs darkest. The color of all parts as above given subject to modification by a more or less strong violet tint from the deeper tissues, this being particularly strong in the head and in the anterior and posterior dorsal plates and particularly in younger or recently moulted individuals.

Body moderate; about eight times longer than width of tenth dorsal plate; strongly narrowed cephalad from tenth dorsal plate and abruptly narrowed caudad of this plate as usual. The cephalic plate sparsely hirsute with long and short bristles, the first dorsal plates being clothed subsimilarly to cephalic plate, the last few plates more sparsely clothed, the median portion of the most posterior being subglabrous; legs clothed more abundantly with shorter, finer hairs among longer and stouter, spinescent bristles which are more abundant on the ventral and lateral surfaces of joints proximad of tarsus; antennae densely subpilose.

Head mostly longer than wide, typically in about ratio 12:11; subrotund, widest near middle of length. Lateral margins strongly convexly rounded at middle, caudad of which they are nearly straight or weakly incurved and converge to the truncate caudal margin with the corners well rounded; conspicuously narrowed in front of middle; anterior margin between antennae from nearly straight to a little incurved. Strongly convexly elevated. A distinctly marked furrow extending from ocellus to ocellus and curving caudad from its ends to middle; on caudal portion of plate two broad and distinct furrows which diverge cephalad to the transverse furrow; a broad shallow median longitudinal impression in front of the suture. Lateral and anterior borders of head commonly depressed.

Ocellus very large; strongly convex; bluish; margin not sharply defined.

Antennae long; attenuated from base, becoming much more slender distad. Articles 39 or 40, when 40 the ultimate articles commonly proportionately shorter; second article much longest as usual; usually the four succeeding the second subsimilar to each other, of moderate size, while the next eight are shorter and likewise similar to each other; articles succeeding the fourteenth longer and more slender and more loosely articulated, with among them in most specimens a regular alternation of two shorter articles with one clearly longer one excepting that the last six are all long.

Prosternum twice as wide as long; the anterior margin arching forward in a semicircle, angularly incised at middle as usual. Prosternal teeth 3+3, small and pale; on each side the two innermost

proximate and often elevated together, the outermost being separated by a wider and deeper interval and the prosternal margin beneath it less produced.

The posterior angles of the ninth, eleventh, and thirteenth dorsal plates strongly produced. Dorsal plates strongly arched; each of the major scuta with five more or less evident longitudinal sulci, two lateral parallel with each side, one median and two intermediate diverging caudad; the two lateral sulci continuous with a transverse depression or furrow (sometimes double) running parallel with and a little cephalad of the posterior margin, corresponding lines often being traceable on the head.

Ventral plates with a number of transverse impressed lines on caudal half, one at middle and one between this and caudal margin ordinarily deeper than the others.

Legs all long, the more caudal ones being conspicuously so and ordinarily elevating the caudal portion of body considerably. Tarsi relatively long, the first joint being much longer than the second. Tibial process present on each leg of the first fourteen pairs.

Anal legs very long and slender, not at all crassate or otherwise specially modified in either male or female.

Last five pairs of coxae deeply furrowed or fluted along caudoventral surface, the furrow being limited by well-chitinized ridges or plates. In these furrows occur the uniseriate, circular pores which in number and arrangement vary from 3, 3, 3, 3, 3 to 3, 4, 5, 5, 4.

Claw of female gonopods large, acute, and weakly incurved. Basal spines 2+2 or 2+3; the flattened, broader surface, conical in outline with the inner one set nearly at right angles to the outer and in ventral view therefore appearing much thinner; both spines usually bent ectad at distal end.

Anal glands conspicuous; the common median passage relatively large.

Length 11.4–12.6 mm.; width 1.5–1.7 mm.; length of antennae 5.6–6 mm.; of anal legs 6–6.5 mm.

*Praematurus*.—Ground color light brown to yellow, but in life this color mostly masked by the violet from beneath. Head appearing purple, often very dark. Antennae light brown or yellow. Ventral plates in life appearing mainly violaceous or lavender.

Antennae composed of from 31 to 36 articles.

Prosternal teeth 3+3 as in the adult.

Coxal pores moderately large; groove shallow; 2, 2, 2, 2, 2–3, 3, 3, 3, 3,

Gonopods short. Claw short and pale; basal spines 2+2 but small, the inner one commonly a short point.

Length of body 8-8.4 mm.; width 1.2 mm.; length of antennae 4.6 mm.; of anal legs 4-4.3 mm.

*Agenitalis* — Stage I. — Color yellowish brown, head darker. Legs and antennae smoky white.

In the one specimen of this stage obtained the forty articles of the antennae are already present, the individual doubtless being exceptional in this regard.

Prosternal teeth minute or obscure.

Ocelli distinct; considerably larger than in the following stage.

Gonopods appearing merely as incipient buds.

Coxal pores 2, 2, 2, 2, 2.

Length of body 5.5 mm.; width .65 mm.; length of antennae 2.5 mm.

*Pullus* — Stage IV. — Last three pairs of legs appearing as pale appressed buds.

General color yellowish. Antennae and legs white.

Ocelli small; colorless.

Coxal pores 1, 1; very small.

Length of body 3-4.6 mm.; length of antennae 2.1-2.5 mm.

LOCALITIES. — Utah (in the Wahsatch Mts., chiefly at elevations from 6,000 up to 10,000 feet above sea-level. Farmington Canyon! City Creek Canyon! Mill Creek Canyon! Neffs Canyon! Little Cottonwood Canyon! Big Cottonwood Canyon! American Fork Canyon! Spanish Fork Canyon! Also in Uintah Mts.); California (Truckee! in the Sierra Nevada).

In the Wahsatch Mts. the species is found at the upper elevations under wood and stones along streams, about springs, and near melting snow, and is not uncommon under the fallen logs of coniferous and quaking aspen woods away from running water. It prefers especially cool and humid situations.

ZYGETHOBIUS SOKARIENUS Chamberlin.

Can. entom., 1911, 43, p. 382.

DIAGNOSIS. — Dorsum reddish brown to chestnut, with head and ultimate segments darker; head uniform in color; legs brown, paler distally, the posterior pairs darker. Head subrotund, longer than wide; widest in front of middle; sides but moderately convexly bulging. Body about eight times as long as width of tenth plate; strongly

narrowed cephalad. Antennae long; articles 38 or 39; articles distad of the sixteenth relatively more slender and more loosely articulated, with shorter ones in pairs alternating with longer single ones but last six all of longer type. Prosternum with anterior margin widely rounding as usual; teeth 3+3. Posterior angles of ninth, eleventh, and thirteenth dorsal plates produced. Coxal pores 2, 3, 3, 3, 3-3, 4, 4, 4, 4; circular and small. Legs long; tibial spur occurring on each leg of the first fourteen pairs. Claw of female gonopods long and acute, moderately curved; basal spines 2+2, distally thin, conical in broader outline, with the inner set at an angle with the outer. Gonopods of male long; ending in an acutely pointed and bristle-tipped process or claw of which the ventral edge is serrate. Length 11-13 mm.

DESCRIPTION.—Dorsum reddish brown or chestnut, with the ultimate segments darker. Head darker than dorsum, uniform. Antennae dark reddish brown proximally, becoming pale distad. Venter from light to dark brown, often of reddish tinge, the posterior segments usually darker. Prosternum usually of same color as venter but sometimes darker, in which case the prehensors are paler, especially distally. Legs usually brown, sometimes dark excepting proximally and distally; the posterior pairs, as usual, commonly darker than the others.

Body moderate; about eight times longer than width of tenth plate; conspicuously narrowed from tenth plate cephalad and abruptly caudad. Sparsely clothed with shorter, finer hairs and with longer coarse spinescent bristles, the latter being more especially arranged in series at lateral and caudal edges of dorsal plates and also across anterior portion of major ones. The bristles more abundant on legs. Antennae densely clothed with straight hairs of which there are short and moderately long ones, the latter becoming reduced from proximal to distal articles.

Head normally longer than wide (12:11, nearly); subrotund, but sides not so strongly convexly bulging as in *dolichopus*; widest in front of middle, from where the sides caudad are substraight or a little incurved to the rounded caudal corners; caudal margin straight; head narrowed cephalad as in *dolichopus*. Head convexly elevated. Conspicuously constricted or furrowed in a semicircle curving caudad from the ocelli; two furrows on caudal portion of plate diverging forward from a common point and on each side of these are several subparallel sulci; a shallow median longitudinal furrow extending caudad between antennae to the transverse furrow. (Plate 4, fig. 5).

Ocelli very large; bluish.

Antennae long, being one half or nearly one half as long as the body. Articles 38 or 39, of which the second is much longer; the fourteen articles succeeding the second are short and closely telescoped, the first four in this series being commonly somewhat larger than the others; articles distad of the sixteenth clearly longer and more freely joined, with shorter ones in pairs normally alternating with single longer ones in the usual way, excepting the six ultimate which are all of the longer type.

Dorsal scuta well arched, with lateral and caudal borders depressed and the lateral margins bent somewhat dorsad; each with a distinct median longitudinal furrow extending entirely across plate; on each side several shorter sulci of which the two most mesal converge together caudad, forming thus a v-shaped mark. Posterior angles of ninth, eleventh, and thirteenth dorsal plates produced. Caudal margins of plates apparently less incurved than in *dolichopus*.

Caudal margin of more anterior sternites truncate, but in the posterior ones more or less convexly rounded. Plates marked with fine transverse furrows of which one caudad of and one cephalad of the middle are usually distinctly deeper.

Prosternum twice as wide as long. Anterior margin semicircular. Teeth 3+3; subequal; the interval between these teeth in some about equal but in others the outer one on each side is more widely removed from the median than the latter is from the innermost. (Plate 4, fig. 6).

Legs of usual type, all being long and having tarsi markedly slender with the first joint especially long. The small, pointed process at distal end on dorsal side of the prefemora better developed and more spine-like on the more caudal pairs of legs. Tibial process present in first fourteen pairs of legs only. (Plate 4, fig. 8).

Anal legs in both sexes long and slender and without special modifications. The lengths of third, fourth, fifth, sixth, and seventh articles are to each other about as 38:41:50:61:28 and their widths as 13:11.5:8:4:3. In the penult legs the lengths of these joints are related as 31:35:41:45:16.

Porigerous surface of last five pairs of coxae but moderately depressed and the furrow typically not extending entirely to distal end of the joint, the lateral walls or chitinous ridges uniting distad of it to form a median keel. Pores circular, decreasing in size proximad; 2, 3, 3, 3, 3-3, 4, 4, 4, 4.

Claw of female gonopods long and acute, but moderately curved,

the ventral edge finely serrate. Basal spines 2+2, flattened distad; conical in broader outline; the inner on each side set more or less at an angle to the outer and its outline in ventral view, presenting its lesser thickness, as a consequence appearing much more slender than the outer. (Plate 4, fig. 4, and Plate 5, fig. 6).

Gonopods of the male long and with same divisions as in the female; ending in a long, straight and acutely pointed process or claw which is bristle tipped and has its ventral edge serrate, this claw but weakly chitinated. Articles densely clothed with long bristles. Penial process subcylindric, running to a point at apex on dorsal side. (Plate 5, fig. 8).

Length 11-13 mm. Males and females apparently not differing in size.

LOCALITY.— California (Mill Valley!).

Of the ten type specimens, four are males.

- *ZYGETHOBIUS COLUMBIENSIS*, sp. nov.

DIAGNOSIS.— Dorsum brown; head dusky; antennae and legs flavid. Head suborbicular; of nearly equal length and width. Body robust, being only about seven times as long as the width of the eighth dorsal plate; strongly narrowed cephalad as in related species. Antennae long; articles 41, the more loosely joined ones beginning with the fifteenth, among them being the usual alternation of shorter and longer ones and the last six all being of longer type. Prosternal teeth very small, 3+3. Posterior angles of seventh, ninth, eleventh, and thirteenth dorsal plates produced. Legs long and slender; tibial spurs present as usual. Claw of female gonopods long and moderately strongly curved; basal spines very acutely pointed, of moderate width at base. Length 14.5 mm.

DESCRIPTION.— Original color difficult to determine from type specimen. At present the specimen is brown, paler along the median dorsal line. Head dusky. Antennae and legs flavid.

Body robust, being about seven times longer than the width of the eighth dorsal plate, the tenth plate being nearly of same width as the eighth; strongly narrowed cephalad from eighth plate to the first which is slightly narrower than the head; third plate manifestly wider than the first. Widths of head and first, third, eighth, tenth, and twelfth dorsal plates to each other about as 40:39:45:56:55:52. First plate 1.85 times wider than long; widest a little cephalad of its

middle, the sides being moderately convex and rounding in well mesad at anterior ends.

Head about equal in length and breadth; suborbicular with the sides strongly convexly bulging caudad of the ocelli. A rather deep transverse sulcus a little in front of caudal edge and two pairs of longitudinal sulci diverging cephalad from this transverse furrow.

Ocelli large; bluish.

Antennae long; extending to or beyond the middle of the body; strongly attenuated distad. Articles 41; of these the first fourteen are relatively more compact as in *dolichopus*, etc., but the transition to the relatively slender and more loosely joined articles more gradual than usual; beyond the fourteenth article shorter articles recur in pairs in the ordinary way, the last six, however, all being of the longer type.

Prosternum twice as wide as long. Teeth very small or almost obscure; 3+3. Margin on each side meeting its mate at very obtuse angle, a mesal incision being scarcely developed.

Posterior angles of seventh, ninth, eleventh, and thirteenth dorsal plates strongly produced; angles of the last three long and acute, while those of seventh have caudal side long and convex, the mesal portion of the plate being deeply incurved. Dorsal scuta strongly arched, with the caudal and lateral borders depressed as usual; each plate with a pair of distinct longitudinal sulci with outside of each one of these a second shorter and more or less divergent sulcus.

Anterior ventral plates broadly depressed from edges to middle. Most plates with indications of three longitudinal sulci of which one toward each side is more distinct than the median. A transverse furrow a little in front of caudal margin especially distinct; one or two more anterior ones present which are less so.

Legs all long with their tarsi conspicuously slender as usual, considerably more so than the tibia which, in turn, is abruptly more slender than the femur. Prefemoral and tibial processes as usual.

Porigerous area of coxa deeply depressed, with the edges well chitimized. Pores circular; about 3, 3, 4, 4, 4, to 4, 4, 4, 4 in number and arrangement.

Claw of female gonopods entire, long and strongly curved, acutely pointed. Spines as usual, acutely attenuated from base distad; of but moderate stoutness.

Length 14.5 mm.; antennae 8 mm. long; width of eighth dorsal plate 2.1 mm.

LOCALITY.—British Columbia (Powder Creek, Kaslo!).

The single type is a female.

## ZYGETHOBIUS PONTIS Chamberlin.

Ann. Ent. soc. America, 1911, 4, p. 34.

**DIAGNOSIS.**—Dorsum chestnut with a narrow longitudinal stripe blackish; first segment darker; head deep or blackish brown; legs brown, paler proximally, excepting last pairs which are darker, being blackish proximally and pale distad. Head subrotund, widest caudad of middle. Body robust; but seven times longer than width of tenth plate; strongly narrowed cephalad and more abruptly caudad as usual. Antennae very long; articles 43; those articles distad of the fourteenth more loosely joined with the usual occurrence of shorter articles in pairs excepting among the last four which are all long. Teeth of prosternum 3+3. Posterior angles of sixth, seventh, ninth, eleventh, and thirteenth dorsal plates produced, those of the seventh least so. Coxal pores circular, small; 3, 3, 4, 4, 4. Legs long and especially slender, distad; tibial process present and well developed on all fifteen pairs of legs.

**DESCRIPTION.**—Dorsum chestnut in color with a narrow longitudinal median stripe blackish; first segment darker than the others. Head deep or often blackish brown. Prehensors, prosternum, and antennae reddish, the last mentioned becoming pale, yellowish distad. Venter yellowish to light brown, with the more caudal plates reddish. Legs brown, paler proximally than distally; last pairs of legs darker, blackish proximally, pale distad.

Robust, being but seven times longer than the width of the tenth dorsal plate. Strongly narrowed cephalad and caudad of the tenth dorsal plate, the first segment being conspicuously narrow. Clothed sparsely with coarse longer hairs and shorter finer ones, the longer ones occurring chiefly along edges of dorsal plates and on the head as spinescent bristles conspicuous among the shorter ones; antennae subdensely clothed with straight hairs and finer shorter ones that are bent or curled at their tips; legs as usual more densely clothed than body.

Head subrotund; widest a little caudad of the middle, the sides caudad of this being nearly straight and converging to the rounded caudad corners; the longer anterior portion of head conspicuously narrowed; anterior margin between antennae straight or mesally a little indented. Head elevated; marked with a transverse furrow or constriction along or a little caudad of the suture, each end of the furrow being in front of the corresponding ocellus; a v-shaped impression consisting of two furrows diverging from a common point cephalad



on posterior portion of head with on each side of this two short sulci parallel to the corresponding arm of the v and on each side parallel with the margin a long furrow extending from a little in front of the caudal margin forward and dorsad of upper edge of ocellus where it joins the transverse furrow or constriction.

Ocelli large but smaller than in *sokarienus*, etc.

Antennae very long, being more than half the length of the body. Articles 43, of which the second is as usual relatively very long, the next twelve being short and compactly telescoped, those distad of these being more slender and more loosely joined; the first ten articles immediately distad of these precede a much longer one which in turn is succeeded by shorter ones than which the four preceding the ultimate are much longer; ultimate article very long. (Plate 5, fig. 9).

Prosternum twice as wide as greatest length or nearly so. Anterior margin semicircularly curved forwards. Teeth 3+3, of which the outermost on each side is more removed than the innermost from the median one.

Dorsal plates with median portion well elevated; a deep wide furrow immediately mesad of each lateral and somewhat upturned margin, a second narrower sulcus occurring a little mesad of this while between this and the median longitudinal furrow are several shorter sulci. Posterior angles of the sixth, seventh, ninth, eleventh, and thirteenth dorsal plates produced, the corners of the seventh being least extended of these.

Ventral plates transversely wrinkled, two to four — but mostly two — of the sulci being conspicuously deeper than the others.

Legs proportioned as in the previously described species, the tarsi being conspicuously slender with the first joint very long. Tibial process present on all fifteen pairs of legs. (Anal leg shown in Plate 4, fig. 9).

Coxal pores small and circular; 3, 3, 4, 4, 4. Ridges limiting the depressed porigerous area of moderate height, the two edges converging to a median keel on distal portion of coxa.

Gonopods of female with claw long, well curved, rather slender and acutely pointed. Basal spines as usual, the inner ones of each pair in ventral view presenting its edge and thus a much more slender outline than the outer one.

Length 10.5–11 mm.

LOCALITIES.— Virginia (Natural Bridge!); Tennessee (Johnson City!).

**PLATE 1.**

Chamberlin: — Hemicopidae of America north of Mexico.

PLATE 1.

LAMYCTES FULVICORNIS Meinert.

- Fig. 1. Mandible.
- Fig. 2. Bipectinate hair or aciculus of same more highly magnified.
- Fig. 3. Ramose or plumose hair from outer branch of first maxilla.
- Fig. 4. First and second maxillae.
- Fig. 5. Tip of palpus of second maxilla.
- Fig. 6. Labrum.
- Fig. 7. Prosternum and prehensors.
- Fig. 8. Ventral view of caudal end of body (female), showing ultimate coxae with their pores, sternite of genital segment and gonopods, and the anal glands.
- Fig. 9. Cross-section through anal glands.
- Fig. 10. Head, dorsal view.
- Fig. 11. Anal leg.
- Fig. 12. Leg of fifth pair, cephalic aspect.

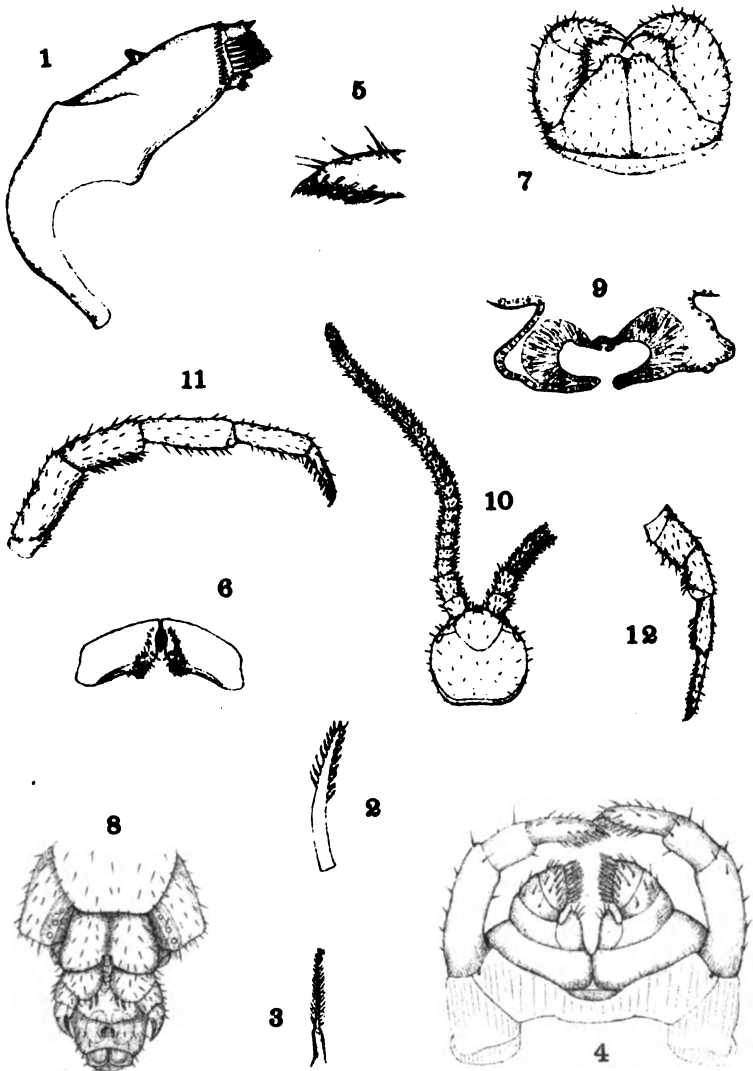




**PLATE 2.**

Chamberlin: — Hemicopidae of America north of Mexico.

PLATE 2.

*LAMYCTES FULVICORNIS* Meinert.

- Fig. 1. Dorsal plates, excepting most anterior.
- Fig. 2. Antenna.
- Fig. 3. Anal leg (from specimen 10 mm. long).

*LAMYCTES PINAMPUS* Chamberlin.

- Fig. 4. Dorsal plates.
- Fig. 5. Antenna.
- Fig. 6. Anal leg (from specimen 8.6 mm. long; same magnification as for fig. 3).

*LAMYCTES PIUS* Chamberlin.

- Fig. 7. Dorsal plates.
- Fig. 8. Anal leg (from specimen 8.5 mm. long; same magnification as for figs. 3 and 6).

*LAMYCTES TIVIVS* Chamberlin.

- Fig. 9. Anal leg (from specimen 6 mm. long; same magnification as for preceding fig.).
- Fig. 10. Antenna.

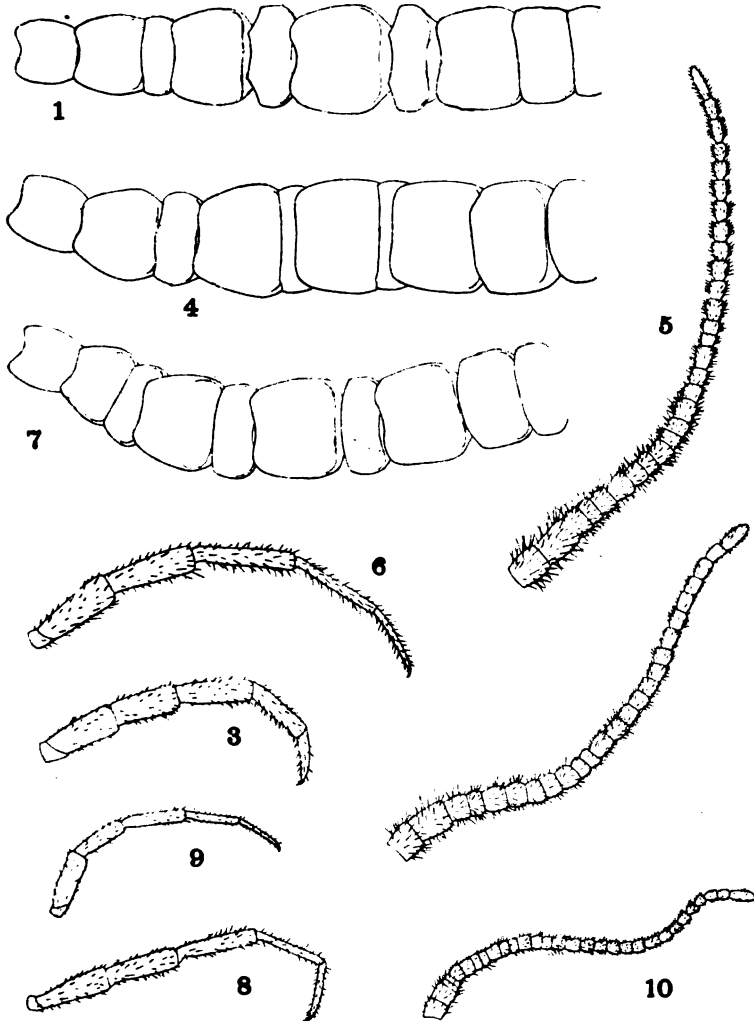






**PLATE 3.**

Chamberlin:— Henicopidae of America north of Mexico.

PLATE 3.

*BUETHOBIVS OABITUS* Chamberlin.

- Fig. 1. Prosternum and prehensors.
- Fig. 2. First maxillae.
- Fig. 3. Mandible.
- Fig. 4. Branched aciculus from tip of outer branch of first maxilla.
- Fig. 5. Ramose or plumose hair from outer branch of first maxilla.
- Fig. 6. Labrum.
- Fig. 7. Head, dorsal aspect.
- Fig. 8. Anal leg.
- Fig. 9. Fifth leg, cephalic aspect.
- Fig. 10. Sternite of genital segment and gonopods of female.

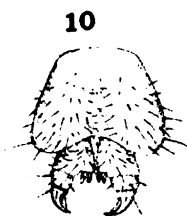
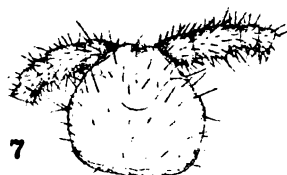
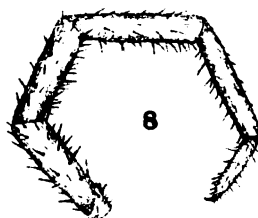
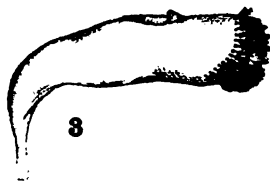
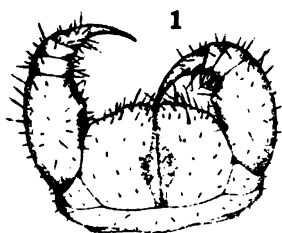




**PLATE 4.**

Chamberlin: — Henicopidae of America north of Mexico.

PLATE 4.

*BUETHOBIUS OABITUS* Chamberlin.

- Fig. 1. Head, ventral aspect, showing organ of Tömösvary.  
Fig. 2. Distal joints of palpus of second maxilla.

*BUETHOBIUS CONIUGANS* Chamberlin.

- Fig. 3. Ventral view of posterior region of body of male, showing gonopods, etc.

*ZYGETHOBIUS SOKARIENUS* Chamberlin.

- Fig. 4. Claw of female gonopods, dorsal aspect.  
Fig. 5. Head, dorsal aspect.  
Fig. 6. Prosternum and prehensors.  
Fig. 7. Anal leg.  
Fig. 8. Leg of fifth pair, cephalic aspect.

*ZYGETHOBIUS PONTIS* Chamberlin.

- Fig. 9. Anal leg.

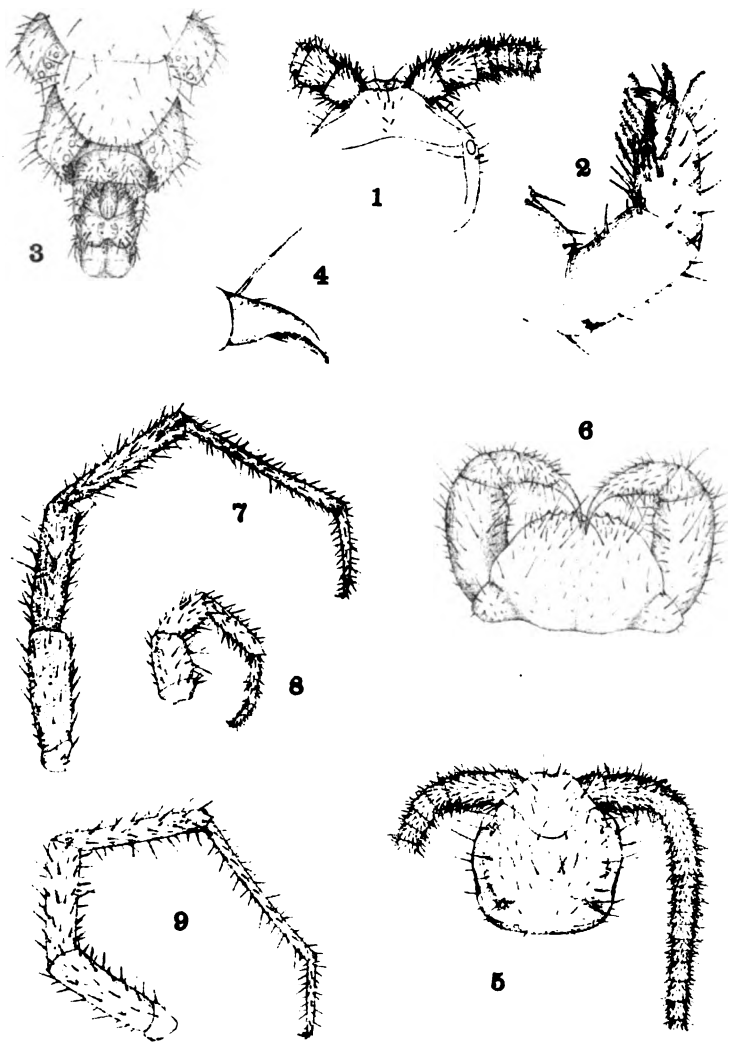






**PLATE 5.**

Chamberlin: — Hemicoptidae of America north of Mexico.

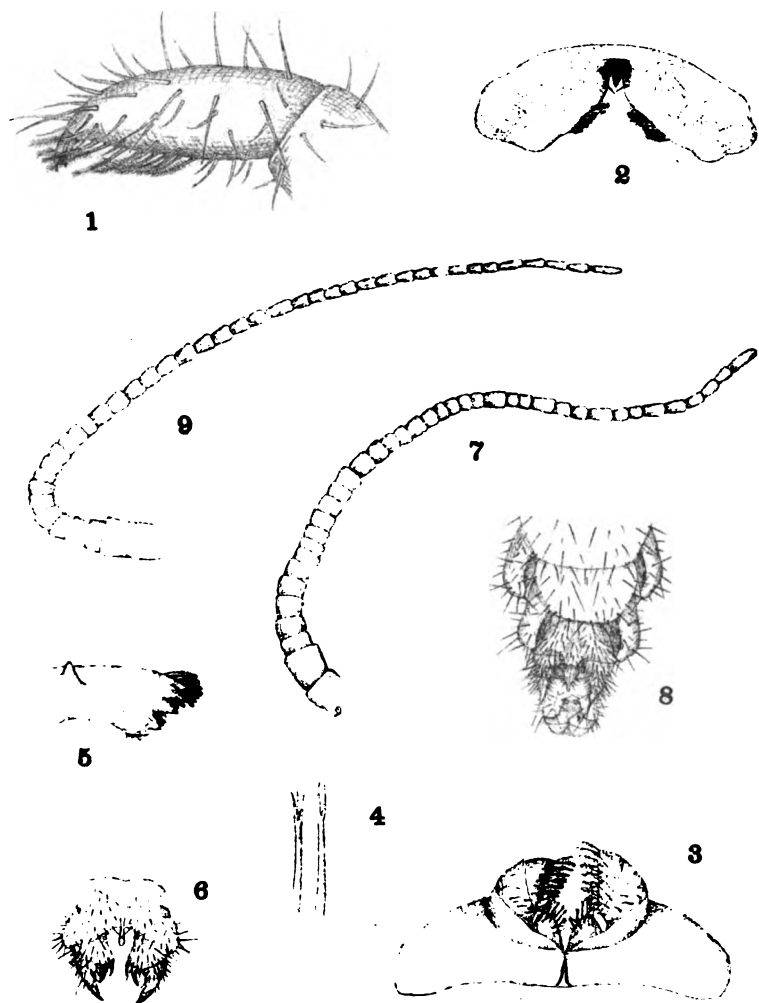
PLATE 5.

*ZYGETHOBIUS SOKARIENUS* Chamberlin.

- Fig. 1. Distal article of palpus of second maxilla.
- Fig. 2. Labrum.
- Fig. 3. First maxilla.
- Fig. 4. Lacinate bristles from inner branch of first maxilla more highly magnified.
- Fig. 5. Mandible.
- Fig. 6. Sternite of genital segment and gonopods of female.
- Fig. 7. Antenna.
- Fig. 8. Ventral view of caudal region of body of male showing gonopods, etc.

*ZYGETHOBIUS PONTIS* Chamberlin.

- Fig. 9. Antenna.









## LYMNÆA COLUMELLA, AND SELF-FERTILIZATION.

BY HAROLD SELLERS COLTON.

The following paper is a preliminary study of the pond snail, *Lymnæa columella* Say, with the particular view of its furnishing material for the study of genetics. We should look to this form because of the probability that when isolated from one another, the eggs that are laid are self-fertilized. No studies have yet been made on animals that reproduce by self-fertilization, so that, as pointed out by Jennings, 1911 B, no work on animals can be directly compared with that on plants.

Notwithstanding the many means by which hermaphroditic animals prevent self-fertilization, a number of cases are well known where normally self-fertilization does occur. As an example of this the following groups may be quoted: Rhabdocoel Turbellarians, Sekera 1906; Polystomum, Zeller 1876;<sup>1</sup> the digenetic Trematodes, Leucart, v. Siebold, Zaddock, Voeltzkow, and others; the Cestodes, Loess, Carlisle, Schultze, Bellingham, van Beneden, Pagenstecher, Leuckhart,<sup>2</sup> and others; the Ascidians *Cynthia* and *Molgula*, Morgan 1904; *Botryllus*, Pizon 1893; and the pond snail *Lymnæa*.

This paper will not discuss the adaptability of the material from the Flat Worms or the Ascidians for breeding experiments. Parasites and marine animals furnish great difficulties at the outset for such a study, and Rhabdocoels reproduce also asexually, so we will turn at once and consider the case of the pond snail.

The first point to be determined is: Does *Lymnæa* self-fertilize its eggs? Oken (1817)<sup>3</sup> isolated an individual adult *Lymnæa*. After an interval of some months this snail laid fertile eggs. Oken concluded that this was a case of self-fertilization. Von Ihring (1876) showed how in many gastropods, *Helix*, for example, a long period, as much as a year, may intervene between copulation and egg-laying. Because of this he did not consider Oken's experiment of any value.

<sup>1</sup> See Bronn, 1899 and 1900.

<sup>2</sup> See Bronn, 1899 and 1900.

<sup>3</sup> See Braun, 1888.



In the meantime von Baer (1835) reported an observation which seemed to confirm Oken's view. He actually saw *Lymnaea auricularia* with own penis inserted in its own female opening. Braun (1888) isolated eggs of *Lymnaea auricularia* in separate vessels and raised the young snails which when they reached adult size laid eggs which developed. Although this author had the snails under observation for weeks and months at a time, he never was able to confirm von Baer. Nevertheless, he did not doubt that von Baer was correct in what he saw. The present writer has repeatedly isolated eggs and had them develop into snails which laid fertile eggs, but has never witnessed a case of self-copulation.

There is the alternative that must be disposed of: Can it be that these eggs are not self-fertilized, but that they develop parthenogenetically? This question cannot as yet be fully answered. To be sure, normal parthenogenesis is unknown in mollusks, but direct evidence on the case in *Lymnaea* is lacking. The reduced number of chromosomes in maturation of the sperm is small, six to eight, but as yet the writer has been unable to satisfactorily imbed the eggs so that they may be cut. As yet he has been unable to observe the first cleavage figures.

An examination of the reproductive organs of the snail will show that there is no reason why self-fertilization should not occur. This system is a complicated one in the lung-bearing mollusks, and *Lymnaea* is no exception to the rule. The eggs and sperm arise side by side in a common ovitestis. When ripe both eggs and sperm pass down a common hermaphrodite duct. Into this duct the albumen gland opens, the function of which is to secrete around the egg a thick coat of albumen. This is the substance which makes the eggs so difficult to imbed. Past this point the duct divides into a thread-like vas deferens with wider portion called the prostate gland, and a thicker-walled oviduct. The former leads finally to an invertible penis just back of the tentacle on the right side of the animal, while the oviduct opens somewhat to the exterior somewhat posterior to the former with a narrow slit. Into the oviduct near its aperture opens the duct from the so-called sperm receptacle, in which the writer has never found sperm, but in which very often he has found eggs. He hopes to deal with this matter at another time.

The reason for describing in some detail the reproductive organs of this animal is to make clear that there is every piece of mechanism present to allow self-fertilization. If the eggs are not fertilized in the upper part of the oviduct, they may be by self-copulation in the lower part.

The fact that self-copulation had been observed by no other observer than the great von Baer, the fact that a case of parthenogenesis is as yet unreported in the group of the mollusks, together with the fact that there is every arrangement present in the animal to make self-fertilization possible—all these seem to the writer sufficient evidence that the chance that parthenogenesis plays a part is remote. This must not be taken as precluding this remote possibility.

Are these animals easy to handle in a breeding experiment? This question may be answered, on the whole, yes.

In 1908 the writer (Colton, 1908) published the results of a series of experiments on the pond snail *Lymnaea columella*, showing the effects of various external conditions upon the growth. Among other things, the writer found how easy it is to raise *Lymnaea* from the egg under ordinary laboratory conditions. They will live in as little as 500 cc. of water and require next to no care. Philadelphia city water from the tap was found to be fatal to the young snails, but the same water, after standing in a large aquarium for some time, could then be used. In his experiments this winter even this water proved fatal, so that water had to be procured from the nearby pond in the Botanical Garden of the University. In the previous experiments a water plant, *Myriophyllum*, and a little soil seemed to offer the optimum conditions for growth, aeration being neglected. This winter the writer has had the best results in using dead leaves of trees from the bottom of the pond referred to above. These were washed in running tap water as a precaution against introducing young snails from the pond. The best results are now procured by using about 700–1000 cc. of pond water in a battery jar and placing in this a half-decayed leaf, such as a maple leaf. One snail only is of course placed in the jar.

The length of time that it takes from hatching to egg-laying varies greatly. As the cause of this variation is not understood at all, it will be at the present time worth while to mention only some of the cases. Thirteen had the following interval from hatching to egg-laying: 32, 26, 35, 49, 58, 92, 50, 50, 56, 57, 63, 74, and 74 days. Twenty-six days was the shortest interval. This shows, even if we neglect the shortest periods, how surprisingly rapid is the growth. As for ease of handling in a laboratory, *Lymnaea columella* is seen to furnish splendid material. They require little care, little space, and come to maturity promptly.

What are the characters that distinguish the various species and

varieties of *Lymnæa* from one another, and what is the character of the variation within one species?

The most recent work on the systematic relationships of the various species and varieties of *Lymnæa* is the monograph on the group by F. C. Baker (1911). This writer recognizes one hundred and two recent species and varieties which he distributes through six genera as follows: *Lymnæa*, two species and three varieties; *Radix*, one species; *Bulimnæa*, one species; *Acella*, one species; *Galba*, fifty-eight species and twenty-eight varieties. The characters on which these genera are distinguished from one another are as follows: the relative size of portions of the male reproductive organs, whether there are one or two penis sac retractors; whether there are two or three cusps on the lateral teeth; proportions of the jaws, length of the spire, axis of the shell gyrate or not, sculpture of the surface, etc. It will be noticed that all these characters, with the exception of two, are purely quantitative. The character of the teeth is a qualitative difference to which the author attributed little importance, as his *Galba obrussa* has the same type of radula as his *Pseudosuccinea columella* when the latter is half-grown. There is no qualitative difference between the radulæ of the adults. Many *Galba* have tri- and other *Galba* have bi-cuspid lateral teeth. Of the one hundred and two species and varieties, of but thirty-two did the writer know aught of the anatomy of the reproductive organs. Nothing is apparently known of the internal anatomy of the type species of the genus *Galba*, that is, *Galba truncatula* Muller. Since the important characters in describing the genera are purely quantitative, the present writer feels that he cannot accept these genera and will for the present consider the old genus *Lymnæa* as including them all. When we know more, some genera may, perhaps, be farther separated. Not being a systematist, the author cannot criticise this work and he is very thankful that someone has taken the trouble to examine all the literature and the species of this interesting group, bringing it together in one work.

The individual species are separated one from the other by quantitative differences in the shell characters, body characters, by color, and where known the genital organs, the radula, and jaw. This roughly outlines the sort of variation that takes place within the genus. Within a single species what can we look for?

In the present case, where selection is hoped to be practiced, characters visible on the exterior can alone be considered. This forbids us at the outset dealing with any characters of the internal

organs. In the snail the shell at once presents itself. So far we have considered the shell alone.

Adams, 1900, made a careful study of the fresh-water prosobranch mollusk *Io* taken from many stations on the same watershed. He measured the height of the spine, the length of the aperture and width of the shell. In the present study three characters were also measured. These were chosen so that when their ratios were plotted a picture of the average shape of the shells of the colony from which the collections were made would result.

The length of the spire of the shell may be expressed by the ratio—altitude to length of aperture. See fig. 1, where  $\frac{AB}{BC}$  this ratio. The width of the shell may be expressed roughly in terms of a ratio, length of the aperture to the width. The former ratio  $\frac{AB}{BC}$  we will refer to as the *ratio*, and the latter ratio we will refer to as the *index*.

Using the measurements furnished by Baker, 1911, which are probably measurements of extreme individuals, calculating their *index* and *ratio* and plotting them, using the *index* as an ordinate and the *ratio* as the abscissa, when these are enclosed by a line, then we have a rough picture of the shape of the shell. Fig. 2 shows such a picture and the dark oval represents *Lymnæa columella* as it occurs about Philadelphia as compared with some forms taken from Baker's measurements.

The writer made a number of collections of *Lymnæa columella* from some ponds and streams about Philadelphia, and also examined several series in the collection of the Academy of Natural Sciences of Philadelphia.<sup>4</sup> The three characters referred to above were measured with proportional dividers, the index and ratio were calculated and plotted in groups. Fig. 3 shows a number of these collections. The

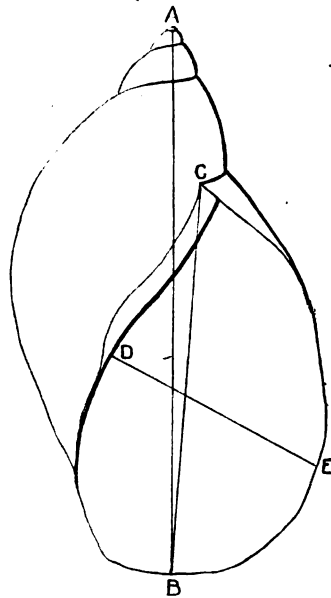


Fig. 1.

<sup>4</sup>The writer wishes to thank Dr. H. A. Pilsbry, of the Academy of Natural Sciences, for many courtesies.

probable error of the single *ratio* and *index* was calculated. These were based on twenty measurements of the three characters from a single shell.<sup>5</sup> The result of this was a probable error of  $\pm .04$  for

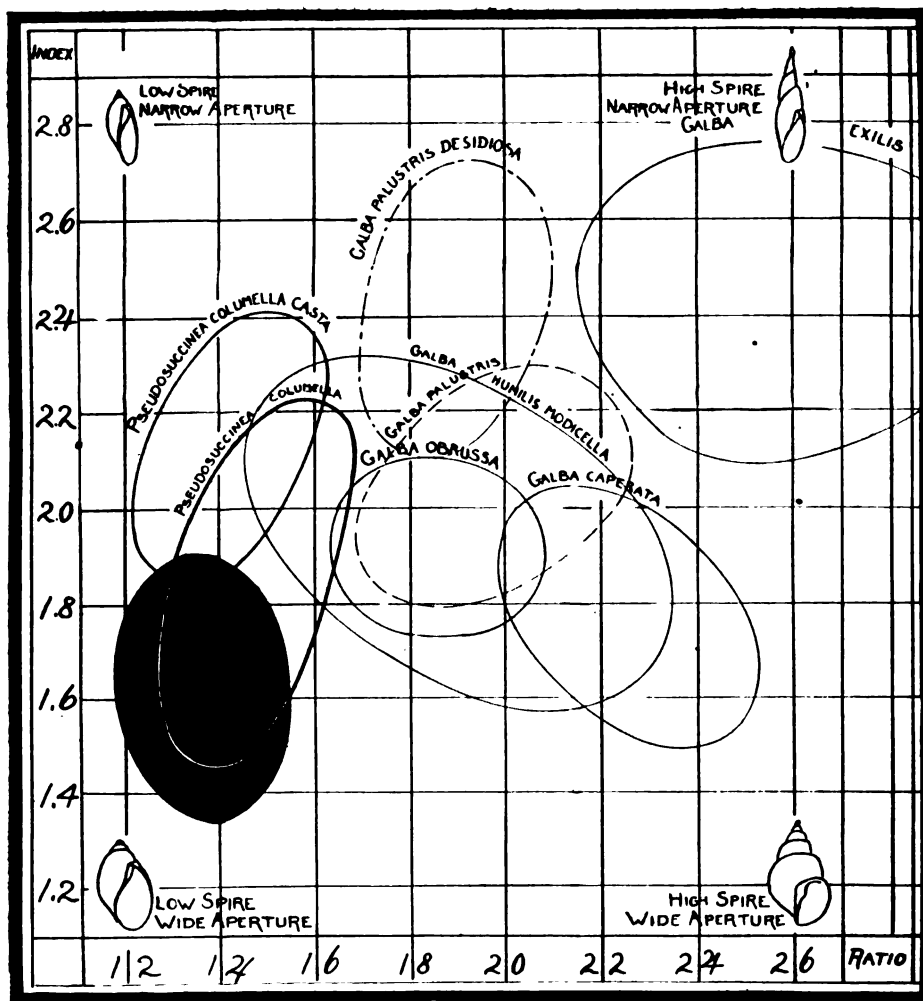


Fig. 2.

the *index* and  $\pm .01$  for the *ratio*. The probable error of the *index* was greater as this character was more difficult to measure. H. B.

<sup>5</sup> See Mellor (1905), pp. 515-520.

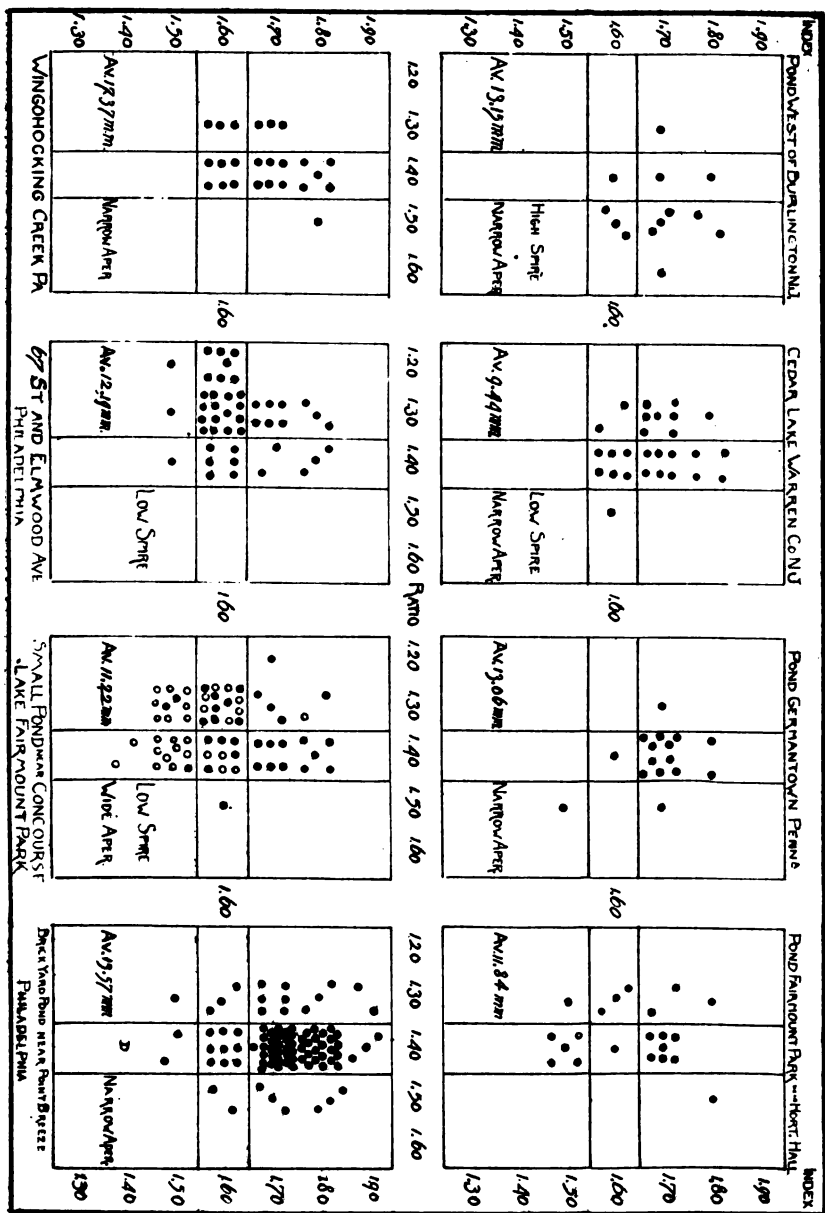


Fig. 3.

Baker (1910) found in *Lymnæa reflexa* that the length-breadth ratio of the shell increased with the length of the shell. That is, the larger shell had the higher ratio and therefore a higher spire. Tables I and II show this relationship in *Lymnæa columella* from about Philadelphia and on both tables the length in millimeters is the

**TABLE I**

TOTAL  
345

| INDEX | 0     | 2     | 4     | 6     | 8     | 10    | 12    | 14    | 16    | 18    | 20    | 22 mm. |
|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|--------|
| 1.90  |       |       |       |       |       | 1     | 2     | 2     |       |       |       | 7      |
| 1.80  |       |       |       |       | 4     | 12    | 16    | 18    | 2     | 3     |       | 55     |
| 1.70  |       |       | 1     | 2     | 14    | 16    | 40    | 25    | 11    | 4     | 4     | 117    |
| 1.60  |       | 1     | 5     | 5     | 17    | 29    | 26    | 14    | 4     | 4     | 1     | 104    |
| 1.50  |       | 2     | 1     |       | 7     | 16    | 12    | 3     |       |       |       | 21     |
| 1.40  |       | 1     |       |       |       | 2     |       |       |       |       |       | 3      |
| MEANS | 1.500 | 1.600 | 1.629 | 1.639 | 1.627 | 1.664 | 1.703 | 1.721 | 1.691 | 1.680 | 1.654 |        |

**TABLE II**

TOTAL  
345

| RATIO | 0     | 2     | 4     | 6     | 8     | 10    | 12    | 14    | 16    | 18    | 20    | 22 mm. |
|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|--------|
| 1.60  |       |       |       |       |       | 1     |       |       |       |       |       | 1      |
| 1.50  |       | 3     | 1     |       |       | 2     | 8     | 6     | 2     |       |       | 22     |
| 1.40  |       | 1     | 4     | 3     | 23    | 39    | 55    | 34    | 7     | 6     | 4     | 176    |
| 1.30  |       |       |       | 4     | 16    | 30    | 26    | 21    | 10    | 5     | 1     | 113    |
| 1.20  |       |       |       |       | 3     | 4     | 5     | 1     |       |       |       | 13     |
| MEANS | 1.475 | 1.420 | 1.343 | 1.348 | 1.332 | 1.373 | 1.373 | 1.358 | 1.345 | 1.380 | 1.362 |        |

ordinate. The *index* on Table I is the abscissa. On Table II the *ratio* is the abscissa. Table I shows that the larger shells have a narrower aperture, which agrees with H. B. Baker, but Table II shows that the height of the spiré is about constant at all ages. On both tables no conclusions can be based on shells under eight millimeters, for two reasons: the numbers of shells are too small and the probable error of each ratio is too large. It may be as much as  $\pm .10$  on the part of the *index* and  $\pm .05$  for the *ratio*.

Remembering, then, that the larger shell may have a narrower aperture, then we may look over fig. 3. In this the Cedar Lake collection and the Wingohocking Creek collection both have narrow apertures, but the former has an average shell of 9.44 mm., while the latter has an average shell length of 17.37. The size of the shell cannot influence, then, the characters in question in this case. The other diagrams tell their own story and seem to show that each restricted area has its own type of shell as far as these two characters are concerned. The numbers are far too small on which to base many conclusions.

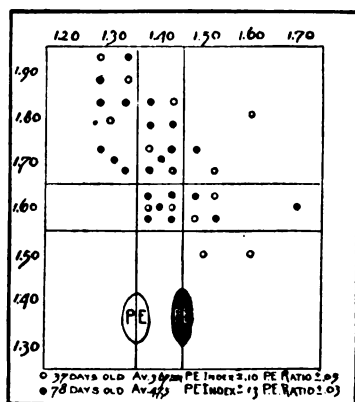


Fig. 4.

There were hatched during the past winter from an egg capsule laid by a snail from the Sixty-seventh Street and Elmwood Avenue collection thirty-two snails, of which eighteen lived to be measured. These were kept together in 1,000 cc. of water in a crystallizing dish. They were measured from time to time. From two of these measurements, an early one and a late one, 37 days and 78 days, respectively, fig. 4 was compiled.

The probable error of the individual 37 days old measurements,



which were made with the camera lucida, were *index*  $\pm .10$ , *ratio*  $\pm .05$ . These were so much larger in the case of the small shells because of the difficulty in orienting them in exactly the same plane at the time of measurement.

The range of the offspring are almost the same as that of the parent colony. This is only significant as showing what we may expect when we are able to deal with larger numbers in a more precise manner.

Baker (1911) observed copulation between different individuals of *Lymnæa stagnalis*, *Lymnæa emarginata* and *Lymnæa lanceata*. Several times *L. emarginata* tried to copulate with *L. lanceata*, a much smaller animal. Baker saw also *L. stagnalis* in copulation with *emarginata*. Heynemann (1869) records a cross between *auricularia* and *peregra*, the former acting as female and the latter as male. Chaster (1909) records a cross between *L. stagnalis* and *L. auricularia*, the former taking the part of the male. The progeny were good examples of *peregra*, and the query is raised by Chaster as to whether *peregra* may not be the ancestral form of *auricularia* and *stagnalis*. Be that as it may, it is possible that many of the so-called species and varieties of *Lymnæa* may be hybrids, and it will be necessary to experiment in order to determine how true this is. In the ponds about Philadelphia, however, where *Lymnæa columella* is found, the writer has never found any other species present. The chance of hybridization is, therefore, rare.

#### CONCLUSION.

Johannsen (1911) clearly defined the "pure line." "A pure line," he said, "may be defined as the descendants from one single homozygotic organism exclusively propagating by self-fertilization. . . . A line ceases to be 'pure' when hybridization (or even intercrossing) disturbs the continuity of the self-fertilization." With this definition in mind it is necessary, if we would have a pure line in the Johannsenian sense, to deal with hermaphroditic organisms. Not only must the organisms be hermaphroditic, but self-fertilization must be possible. It must either be normal or can be induced and controlled. These conditions can easily be fulfilled in many plants, but, as far as I am aware, no animals with the proper requirements have been experimented upon.

To be sure, Jennings (1911) and others have traced "lines" of Protozoa. These animals divide by fission so that their method of reproduction is probably closely allied to asexual or to parthenogenetic reproduction as found in multicellular forms.

The *Hydra* with which Handel (1907) worked reproduced by

budding. On the other hand, Woltereck's (1909) *Daphnia* were parthenogenetic. These "lines" of animals therefore cannot be compared strictly with those "lines" in plants that reproduce through self-fertilization.

Adhering strictly to Johannsen's definition, as far as I know no experiments with *pure lines* have ever been performed with animals.

*Lymnæa*, after this superficial study, would seem to furnish such material:

1. It apparently does self-fertilize its eggs when isolated.
2. The time for generation is short—two to three months.
3. There are a few well-defined characters that may be observed.
4. Hybridization is possible, but as far as *Lymnæa columella* from this region is concerned, it is rarely that more than one species is found in a single habitat. There is no evidence, as yet, that it is not homozygous.

On the whole, *Lymnæa columella* seems to combine some of the necessary requirements on which to base a pure-line investigation.

#### LITERATURE.

- ADAMS, C. C. 1900. Variation in Io. *Proc. of the Am. Ass.*, IL, 208.
- VON BAER. 1835. Selbstbefruchtung an einer hermaphroditischen Schnecke beobachtet. *Müller's Arch. f. Anat. u. Phys.*, Jahrg. 1835, 224.
- BAKER, F. C. 1911. The Lymnæidæ of North and Middle America. *Chicago Academy of Sciences*, Publication No. 3.
- BAKER, H. B. 1910. Variation in *Lymnæa reflexa* Say from Huron County. *Twelfth Report of the Mich. Acad. of Sci.*
- BRAUN. 1888. Zur Frage der Selbstbefruchtung bei Zwitter Schnecken. *Nach. d. deutsch. malakozol. Ges.*, XX, 146.
- BRONN. 1889 and 1900. Klassen und Ordnung des Tierreichs.
- CHASTER. 1899. A Cross between *Lymnæa stagnalis* and *L. auricularia*. *Jour. of Conch.*, IX, 282.
- COLTON. 1908. Some Effects of Environment on the Growth of *Lymnæa columella* Say. *PROC. ACAD. NAT. SCI. PHILA.*
- HANDEL. 1907. Vererbung bei ungeschlechtlicher Fortpflanzung von *Hydra grisea*. *Jenaische Zeitschr.*, XLIII, 321.
- HEYNEMANN. 1869. Begattung zwischen *Lymnæa auricularia* und *peregra*. *Nach. d. deutsch. malakozol. Ges.*, I, 37.
- VON IHRING. 1876. An unsere Mitglieder. *Nach. d. deutsch. malakozol. Ges.*, VIII, 49.
- JENNINGS and HARGITT. 1910. Characteristics of the Diverse Races of *Paramecium*. *Jour. of Morph.*, XXI, 495.
- JENNINGS. 1911. "Genotype" and "Pure Line." *Science*, December 15, 841.
- JOHANNSEN. 1911. The Genotype Conception of Heredity. *American Naturalist*, XLV, 129.
- MELLOR. 1905. Higher Mathematics for Students of Chemistry and Physics.
- MORGAN. 1904. Self-fertilization Induced by Artificial Means. *Jour. of Exp. Zool.*, I, 135.
- PEARL. 1911. Inheritance of Fecundity in the Domestic Fowl. *American Naturalist*, XLV, 321.
- PIZON. 1893. Histoire de la Blastogénèse chez les Botryllides. *Ann. des Sci. Natur.*, XIV, 1-386.
- SEKERA. 1906. Ueber die Verbreitung der Selbstbefruchtung bei den Rhabdocoliden. *Zool. Anz.*, XXX.
- WOLTERECK. 1909. Verhandlungen deutsch. zoologischer Gesellschaft, 1909, 115.



## DEPARTMENT OF MARINE BIOLOGY.

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### *Physiological Studies on the Protozoan Parasites of Diadema setosum,* by Dr. Merkel H. Jacobs, University of Pennsylvania.

The object of these experiments was to determine how far, in the case of a number of forms of parasitic protozoa, presumably of different origin, inhabiting the same host, the similarity of their environment has brought about physiological similarity in the parasites. The method employed was to determine and compare the resistance of each of the forms in question to various artificially changed conditions. The protozoa chosen for the purpose were the ciliates parasitic in the alimentary tract of the large black sea-urchin, *Diadema setosum*. They are comparatively unspecialized forms, which are easy to obtain in large numbers, and are therefore suitable for the beginning of such a study. The writer intends to extend the results obtained by a series of similar experiments on some of the more specialized forms found in other animals.

The protozoan parasites of *Diadema* are chiefly ciliates, of which four kinds are by far the most abundant. These four forms are not closely related to each other and differ widely in size and structure. Since apparently none of them have been described or named, they are designated in these experiments, for purposes of convenience, by the letters A, B, C, and D. Form B seems to be present in almost, if not quite, 100 per cent of all adult diademas, C in about 75 per cent, D in about 40 per cent, and A in about 33 per cent. The number of individuals present is often very large. The parasites seem to be confined exclusively to the alimentary tract, and are found chiefly in the upper coil of the intestine. Very young diademas do not contain them and slightly older specimens, while sometimes showing forms C and D, and another form not found in the adult (?), do not seem to contain either A or B. None of the forms in question was ever found in sea-water nor in unrelated animals, although a careful search was made for them. In other genera of sea-urchins, however, they may occur in varying numbers. B was found rarely in *Toxopneustes* and *Echinometra*, and C on a number of occasions in *Toxopneustes*, while D seems to be present in every adult *Toxopneustes*, which probably is its true host, and rarely in *Echinometra*. A was never found outside of *Diadema*. A number of specimens of *Hipponoe* were examined for protozoan parasites, without results.

The experiments made to throw light on the physiological resemblances and differences of the forms in question dealt with the following points: (1) ability of parasites to live outside the body of the host; (2) ability to

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[Extracted from Year Book No. 10 of the Carnegie Institution of Washington, pages 131-133.]

live in the body-fluid of other related animals; (3) ability to live in the body of the host after the death of the latter; (4) resistance to high temperatures; (5) resistance to  $\text{CO}_2$ ; (6) resistance to  $\text{H}_2\text{S}$ ; (7) resistance to decomposing proteids; and (8) resistance to acids and alkalis. The following results were obtained:

All of the forms experimented on can live for a certain length of time outside the body of *Diadema*, either in the body-fluid of the latter or in sea-water. Form A lives in sea-water only 2 or 3 hours, D about 24 hours, C a trifle longer, usually less than 30, while B lives for 2 or 3 days. The different forms therefore show considerable differences in their resisting powers, B being about 24 times as resistant as A.

The exclusion of air from a sea-water culture by boiling the water before using it and keeping the culture in a tightly sealed dish has a favorable effect on B, increasing its life to as much as a week, which is the longest period for which any of the four forms have been kept alive in artificial cultures. A, C, and D are scarcely affected one way or the other by this treatment.

The body-fluid of *Toxopneustes* seems to be toxic to the parasites of *Diadema* and *vice versa*. Placed in a few drops of *Toxopneustes* body-fluid, form A from *Diadema* died in an hour and a half, B in 3 hours, and C was living after 15 hours, but dead in 24. In the control culture in which the same forms were kept in the body-fluid of *Diadema*, both B and C were alive after 15 hours and B after 24. C therefore lives almost or quite as long in the body-fluid of *Toxopneustes* as in that of *Diadema*, while B lives something less than one-eighth as long. Form D from *Diadema* unfortunately was not available for this experiment. The same form from *Toxopneustes* was killed by the body-fluid of *Diadema* in 1 to 2 hours. There are good reasons for believing that mere differences in the concentration of the two body-fluids can not account for the facts observed, but that chemical rather than physical factors are involved.

The four parasites behave differently after the death of the host. D disappears as a rule in 12 to 15 hours, A in less than 20, and B and C often live as much as 24 hours. None of the forms, however, have been found living after 30 hours; a diminution in the numbers of all can frequently be detected in less than 12.

A is killed by a temperature of  $39.5^\circ \text{C}$ ., while B and C both succumb at about  $40.5^\circ$ . Figures for D are not available.

The forms in question show their most striking differences in their resistance to chemicals. Experiments were made with a number of substances which they either might be expected to encounter in nature ( $\text{CO}_2$ ,  $\text{H}_2\text{S}$ , decomposing proteids), or which were at least representatives of a class of such substances ( $\text{H}_2\text{SO}_4$  and  $\text{KOH}$  as representatives of acids and alkalis).

Placed in a gas-chamber filled with pure  $\text{CO}_2$ , D is killed in 3 to 4 minutes, A in 5 to 6, C in about 15, and B in 45 to 60. B is therefore about 15 times as resistant as D. Water saturated with  $\text{CO}_2$  has a similar effect.

Treated in the same way with  $\text{H}_2\text{S}$  (which can be detected in the intestine of *Diadema* soon after death), C is killed in 1 to 2 minutes, D in about 3, A in 3 to 4, and B in 10 to 15. B is therefore 8 to 10 times as resistant as C.

Of an infusion made by allowing fragments of *Diadema* tissues to decay in sea-water for 3 days, 5 drops were added to 10 drops of a culture containing the four forms in question. B was killed almost instantly, certainly in less than 5 seconds, A in 10 to 60 seconds, D in 20 to 25 minutes, and C only after about 2 hours. C is therefore 1,500 times as resistant as B.

Treated with  $H_2SO_4$  in the proportion, 1 drop of N/10 acid to 5 of culture fluid, A is killed in about 5 seconds, D somewhere between 5 and 30, the exact time not being noted, C in about 30 seconds, and B only after an hour and a quarter. B is therefore 900 times as resistant as A and 150 times as resistant as either C or D.

The effect of KOH of the same strength is quite different. A is killed in 2 minutes, D in something less than three-quarters of an hour, B in about 1 hour, and C in 3 to 4 hours, C being about 100 times as resistant as A and 3 to 4 times as resistant as B.

The general result of these experiments is to show a surprising difference in the resisting powers of the parasites of *Diadema* to various changed environments. In some cases the most resistant form may live several hundred times as long as the least resistant. Furthermore, a form which is strongly resistant to one condition may be only feebly so to another, and *vice versa*. For example, B is 8 to 10 times as resistant to  $H_2S$  as C, but 1,500 times *less* resistant to the products of proteid decomposition. C is more resistant to  $CO_2$  than A or D, but less resistant to  $H_2S$ . A, C, and D are 24 to 450 times more resistant to KOH than to  $H_2SO_4$ , while B is somewhat *less* resistant, etc. These and other similar facts that might be adduced show that each of the forms in question has certain physiological traits that are almost as characteristic and well-marked as its morphological ones. Furthermore, so far as the evidence obtained from these experiments goes, there is no reason to suppose that the similar habit of life in the parasites of *Diadema* has succeeded in bringing about physiological similarity, except in such adaptive characters as are necessary for existence within the same host.



## STUDIES ON THE PHYSIOLOGICAL CHARACTERS OF SPECIES

### I. THE EFFECTS OF CARBON DIOXIDE ON VARIOUS PROTOZOA

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#### I. INTRODUCTION

Considering its importance in connection with many aspects of modern biological research, the question of the physiological characters of species, as opposed to their morphological ones, has received a surprisingly small amount of attention. This condition has doubtless resulted partly from the fact that physiological characters, on account of their less definite and tangible



nature, are more difficult to deal with than morphological ones, and partly from the fact that single physiological characters at least, are notoriously unreliable guides in the questions of classification and phylogeny that up until the present day have occupied so large a share of the attention of working biologists.

The latter objection, however, no longer holds today, at least to the same extent that it formerly did. Modern zoology is not so much interested in finding out what are the probable relationships of a given animal as in learning what it is, and especially what it *does*. This is the physiological point of view, which is uppermost in the minds of most biologists today. No data which throw light on what goes on in the living organism are any longer considered unimportant; indeed, they are coming to be recognized as a vital necessity. If our knowledge of comparative physiology were as complete as our knowledge of comparative morphology, for example, there is not a single one of the more modern developments of biological science that would not have its possibilities enormously extended. It is therefore a matter of increasingly great importance to accumulate accurate data on the physiological characters of organisms, to determine which ones are fundamental, and which accidental, which are constant in a given species, or larger group, and which vary in different individuals of the same species, or perhaps in the same individual at different times; in short to obtain as full and comprehensive a knowledge as possible of the physiological characters of organisms. Perhaps the day may come when it will be possible to define any species in physiological and chemical terms in the same way in which it is now defined in morphological ones, and when no description of an organism will be considered complete which does not include its chief physiological peculiarities along with its structural one. The biologists of that day will be able successfully to attack problems that for the present must remain untouched on account of lack of the proper kind of knowledge.

It is needless to state that many observations of the sort suggested have already been made. Not to mention the more or less scattered ones made on many widely separated groups of organisms, we already have a considerable knowledge of the

physiological characters of many of the bacteria, a group in which, for obvious reasons, our physiological knowledge has far outstripped our morphological knowledge. Botanists have also accumulated an enormous fund of knowledge relating to the comparative physiology of the green plants, while in such special fields as the study of the blood sera of the higher vertebrates, to give but one example, encouraging progress has been made. Nevertheless, it is apparent that very little has been done in the way of systematic studies along the lines suggested, with the ultimate object of making the physiological characters of each organism as well known as its morphological ones. Such an undertaking is not the work of one man or of one generation. Many years must elapse before our knowledge will be anything but exceedingly fragmentary and scattered. The following paper is therefore a very modest contribution to so large a subject. It deals merely with the effects of a single common and important substance, carbon dioxide, on a number selected protozoan forms, with especial reference to their movements and general vitality. It will be followed at intervals by other papers on the effects of various other substances, so far as possible on the same forms. It is not claimed that the results are, or will be, complete or exhaustive; still it is hoped that they may not be without interest and a certain amount of value.

## II. MATERIAL AND METHODS

The forms studied were various of the most common ciliate Infusoria and flagellates, i.e., *Paramecium caudatum*, *P. aurelia*, *P. bursaria*, *Colpidium colpoda*, *Coleps hirtus*, *Blepharisma lateritia*, *Euplotes patella*, *Vorticella nebulifera*, *Peranema trichophorum*, *Euglena viridis* (?), *Chilomonas paramecium*, and *Entosiphon sulcatum*. In the case of all the forms mentioned except the last one, observations were made on individuals from several different cultures of different origin, the intention being to obtain, so far as possible, data which would apply to the species as a whole and not simply to a particular race. Of course it will be necessary to extend the observations still further before draw-

ing absolutely final conclusions; it is thought, however, that further work will not materially alter the results arrived at in this paper.

The general method employed in studying the effects of carbon dioxide on the forms in question was to subject them, in a drop of culture fluid, to a continuous stream of this gas in an Engelmann gas chamber. The drop of liquid containing them was placed on a slide or cover glass and the latter inverted in the usual way over the opening of the gas chamber, the joints being made airtight with vaseline. The observations were made entirely with the compound microscope, chiefly with a Leitz 3-objective, although in doubtful cases the 7-objective was also employed. The points especially noted were the time required to stop normal locomotion, the time required completely to stop the beat of the cilia, flagella, etc., and the longest possible exposure after which recovery is possible when normal conditions are restored. In addition, incidental observations were made on the general behavior of the organisms and the visible structural changes produced in the cell by carbon dioxide.

The gas used in the experiments was generated in the apparatus designed by McCoy, from marble and C. P. hydrochloric acid diluted in the proportion of one part of acid to four of water. Before coming in contact with the animals it was passed through two wash bottles filled with a solution of sodium carbonate to remove any traces of hydrochloric acid that might be present and also to ensure thorough saturation with water vapor. That no appreciable amount of hydrochloric acid was left in the gas was shown by conducting it into a silver nitrate solution, which in the course of two hours showed no traces of a precipitate or even of a cloudiness. The gas after being thus purified was conducted successively through four Engelmann chambers, each placed on the stage of a microscope, and connected by rubber tubing in such a way that the same gas passed through all of them. This arrangement was found very useful, not only in making comparisons between different species under as nearly identical conditions as possible, but also in facilitating a larger number of independent observations on individuals belonging to the same species.

Preliminary experiments showed the necessity of observing a number of precautions. The first of these is that the rate of evolution of the carbon dioxide gas shall be approximately the same in different experiments which it is desired to compare, since it was found that, other things being equal, the slower the stream of carbon dioxide passing over the drop the longer the animals survive. This is probably due to the fact that in a rapid stream the air is removed from the gas chamber and the drop more quickly, and the animals have less time to adjust themselves to the new conditions than in the case of a slow stream. By using all four of the gas chambers in one experiment it was found easy to compare a considerable number of forms with this factor constant. Frequently, indeed, a number of forms were present in the same drop and thus subjected to exactly the same conditions. In order to be able to compare experiments made on different days the attempt was made always to have the gas evolved at the rate of approximately 100 cc. per minute. This it was found possible to do within the necessary degree of accuracy by proper regulation at the beginning of the experiment of the apparatus, which is automatic when once started.

A second and most important point to be considered is the temperature, which has a marked effect on the time in which death occurs. A preliminary experiment on the three species of *Paramecium* showed that at 22°C. death occurs in roughly half the time in which it does at 12°C. In order that this factor might be made constant, all of the experiments here recorded were made at, or very near, the first mentioned temperature, which is slightly above ordinary room temperature.

A third point that cannot be neglected is the size of the drop containing the animals. Preliminary experiments showed that this has an appreciable effect on the results obtained, especially when the drop is very small. In one such experiment in a very small drop the average time of death of a certain 'pure' race of *Paramecium aurelia* was seventeen minutes while the average for the same race in a rather large drop was thirty minutes. In two medium sized drops in the same experiment the times were twenty-eight and twenty-nine minutes respectively. It will be

seen therefore that while there is not very much difference between the medium sized drops and the large one, the small one shows a decided difference. This is probably due to the greater suddenness with which the animals were subjected to the carbon dioxide in the latter case rather than to any difference in its concentration ultimately in the drops, since these probably all became practically fully saturated long before the end of the experiment. In order to guard against this source of error the drops were all made as nearly the same size as possible, the standard being a drop about 8 mm. in diameter with a moderate curvature. Results obtained in this way were constantly compared with those obtained when a number of the forms in question were present in the same drop.

The final precaution has already been mentioned, namely, not to base far-reaching conclusions on results obtained from a single culture. In the case of some of the forms studied more than a dozen cultures were employed; in all of them except one form, obtained very late, the number of cultures was at least three.

### III. OBSERVATIONS AND EXPERIMENTS

#### A. *Ciliates*.

1. *Paramecium caudatum*. The effects of carbon dioxide on this form are briefly as follows. Immediately after the current of gas has been turned on, the animals exhibit a general restlessness and begin to seek the center of the drop, or rather, to avoid its edges, doubtless because the concentration of the carbon dioxide is greatest there. Inside a minute, as a rule, in a drop of the size used in these experiments, they have collected in its central and thickest part. Here they swim about actively but in very short paths, since the 'avoiding reaction' occurs whenever their movements have a tendency to carry them into the thinner and consequently more saturated part of the drop. Soon, however, generally within two or three minutes, they cease to be able to discriminate between the concentrations in different parts of the drop and spread out again until they are uniformly distributed. Sometimes toward the end of the experiment, for unknown reasons, they collect about its edge. Previous workers have noticed the

behavior just described. Loeb and Hardesty ('95) mention that *Paramecium aurelia* remains in the center of the drop fifteen minutes. In all probability they were dealing with a larger drop than the one used in these experiments, where in no case did either *P. aurelia* or *P. caudatum* require more than a few minutes to become adjusted to the new condition.

After this primary response, the animals swim about in a more or less normal manner but more and more slowly, until they finally come to rest in a time that may vary from twenty or twenty-five minutes to several hours. Even after locomotion has ceased the cilia continue to beat for some time. As death approaches they beat slowly and irregularly and frequently show visible signs of injury. Often a group of them may keep on beating after the others have come to rest. There seems to be nothing constant about the part of the body where movements persist longest. After the cilia have completely stopped it seems to be impossible to start them again even by prolonged exposure to the air. The animals are to all intents and purposes dead. The same thing is true of the other ciliates studied, with the exception of *Vorticella*, whose membranelles are often stopped before the animal is seriously injured and consequently can be started again. In the majority of ciliates, however, the vibratile structures are among the most resistant parts of the cell and when they have finally succumbed the life of the rest of the cell is practically extinct.

In the meantime, certain other changes have been occurring. Among the most striking of these is the change in shape of the body, which becomes shorter and thicker. Some of the increase in the thickness is doubtless due to the shortening, but this does not account for all of it, and it is probable that an actual increase in volume occurs by the absorption of water. This phenomenon is more strikingly shown in some of the other forms studied than in *P. caudatum*. About the time that the swelling becomes noticeable, the nuclei begin to be very clearly visible, standing out sharply from the rest of the protoplasm by their greater opaqueness. This is perhaps due to the acid nature of the medium surrounding the cell since other acids produce the same phenomenon. A further effect of the carbon dioxide often is apparent in the burst-

ing of the pellicle and the flowing out of droplets of clear protoplasm. This may occur either before or after the cilia have stopped beating, but is not so constant in *P. caudatum* as in some of the other forms studied. There is reason to believe that this result is at least partly due to actual injury of the pellicle and not merely to an increase of internal pressure, since the bursting sometimes occurs when the cell has not markedly swollen and also never appears until late, while the cell may reach almost its maximum volume quite early. Furthermore, after one droplet has formed, thus supposedly relieving the internal pressure, others may form in quick succession at other parts of the cell boundary. This effect is not a specific one of carbon dioxide since Budgett ('98) noted the same phenomenon in *Paramecium* and other protozoa when merely deprived of oxygen in a stream of hydrogen, and high temperatures also cause the same result.

The time that elapses from the beginning of the experiment until the death of the animal varies considerably with circumstances. The lowest average obtained in a single experiment was about twenty minutes, the highest over three-and-a-half hours, more cultures, however, approaching the latter value than the former. In an effort to determine to what extent *P. caudatum* can be said to have a specific resistance especial attention was paid to the question of the amount of variation shown by different individuals, races and cultures. A large mass of data was accumulated which will be made the basis of another paper on a somewhat different subject. It may not be out of place, however, to say here that while there is some evidence that different races may have different powers of resistance, these differences are insignificant compared with the enormous changes in resistance that a single race may undergo under appropriate changes in the culture medium. It is possible artificially to change the resistance very greatly, and such changes also occur naturally during the ageing of the culture, an old culture in general having a high resistance, and animals kept in the laboratory for a time being more resistant than 'wild' ones. Great as these variations are, however, they have their limits and in the dozens of cultures and thousands of individuals studied none were found which had as low a resist-

ance as the average *Coleps hirtus* for instance, or as high a one as the average *Colpidium colpoda*. Furthermore in a given culture, if *P. caudatum* has a higher resistance than usual, the other forms present also will, and their relative resistance remains practically constant. It is possible, therefore, to attribute to *P. caudatum* as well as to the other forms a specific resistance, remembering only that its absolute value is somewhat subject to variation under different conditions and that in comparing different forms it is well to have them either from the same culture or at least to make a considerable number of independent observations on different cultures.

2. *Paramecium aurelia*. A comparison of this form with the preceding one will illustrate the statement just made. *P. aurelia* is in general considerably less resistant than *P. caudatum*. When the two forms are present in the same culture the former is always killed sooner than the latter, though rarely, when different cultures are studied, some strains of *P. aurelia* are encountered which show a higher resistance than some of the most susceptible strains of *P. caudatum*. In general, however, *P. aurelia* is killed in less than a half hour while *P. caudatum* nearly always survives several times as long. The average time of death in the two extreme experiments on *P. aurelia* was a little over ten minutes on the one hand and over two hours on the other, in most of the experiments, however, lying, as already stated, below thirty minutes. Loeb and Hardesty state that *P. aurelia* is killed by carbon dioxide in two-and-a-half to three-and-a-half hours. Perhaps their culture was an abnormally resistant one, or possibly the application of the gas was slower than in these experiments, or the temperature lower. In view of the fact, however, that the figures given by them are quite typical of the rather more common *P. caudatum* at ordinary room temperature, and also that the distinction between *caudatum* and *aurelia* formerly was not very sharply drawn, it is possible that they were dealing with the former rather than the latter species. The difference in size between the two forms is probably not the reason for their different powers or resistance, since in the same species no constant relation could be found between the time of death and the size of the animal. Further-



more, the larger *P. busaria* is *less* resistant than *P. aurelia* and the somewhat smaller *Colpidium colpoda* far more resistant. The cause of the difference is evidently of a more deep seated nature.

In the general effects produced on it by carbon dioxide, *P. aurelia* closely resembles the preceding species. It shows the same negative response at first, which disappears in about the same time. The body swells in about the same way. The nuclei often become very distinct, and this fact frequently renders an accurate identification possible without staining. The interval between the time when locomotion ceases and the cilia stop beating is both relatively and absolutely shorter than in *P. caudatum*. There is also a much greater tendency for the pellicle to rupture, this occurring in some cultures in almost every individual. Perhaps this apparently greater delicacy of the body wall may be correlated with the lower powers of resistance of this form.

3. *Paramecium bursaria*. In a number of the cultures used in these experiments this species was found associated with the two preceding ones and therefore a favorable opportunity was presented to compare it with them. Such a comparison shows that it is the least resistant of the three. The average time of death was generally ten to twenty minutes, though in a number of cultures it was less than five and only rarely ran as high as thirty. The most resistant *individual* found lived over an hour but this was a most exceptional case. (It was in this culture that *P. aurelia* also showed its highest resistance—over two hours.) When the three forms in question are present in the same culture in every case observed the relative resistance was: *bursaria*, *aurelia*, *caudatum*, and might perhaps be represented numerically very roughly as 1:2:4. The general effects of the carbon dioxide on this form are on the whole similar to those already described in the case of the other two species. The pellicle apparently is very delicate and nearly always ruptures while the cilia are more markedly affected than those of the other species; as their movements cease they become matted together and very quickly become partly disintegrated, being represented only by an indistinct zone about the animal. It is rather interesting that this green form is less resistant than the colorless ones. Doubtless

on account of the presence of chlorophyll in its body it is accustomed to rather a low concentration of carbon dioxide, since this substance is constantly being removed by it from the surrounding medium. Experiments to determine whether it was more, or less, resistant in bright light than in the dark have as yet not given very positive results, chiefly on account of the difficulty of controlling the temperature factor.

4. *Colpidium colpoda*. This in every case proved to be the most resistant species studied, living long after the other forms in the same drop had succumbed. The general effects on it of the carbon dioxide are as follows. When the stream of gas is turned on a strong negative response is shown and the animals collect in the center of the drop in the same manner as the forms already mentioned; soon, however, they become uniformly distributed and thereafter behave normally almost to the time of death which hardly ever occurs in less than six hours, and may take place much later. In a number of experiments the carbon dioxide was allowed to flow for six or seven hours and was then shut off without however admitting the air, and the animals were found to be in a normal condition the next day. In one such experiment they remained alive for a week, but this experiment was somewhat vitiated by the fact that a small quantity of chlorophyll derived from disintegrated *Euglena* cells was present in the drop, and during the hours of daylight could have furnished a certain amount of oxygen, though only a small portion of the carbon dioxide in the chamber could have been gotten rid of in this way. However, even if these last results be discarded the fact remains that *Colpidium* is exceedingly resistant to carbon dioxide and may remain alive in a drop saturated with it for many hours. Prowazek ('03) found in an experiment of a different sort that *Colpidium* survives a simple lack of oxygen far better than *Paramecium caudatum*.

Carbon dioxide is not without its effects on *Colpidium*, however. Locomotion, while not so markedly affected as in most of the other forms, nevertheless becomes less active than normally. Before death occurs the animals become quiescent, often at the edge of the drop, and the cilia beat more and more slowly until they stop. One point of interest is that the animals, while they

move about in a fairly normal manner appear to take no food, and the food vacuoles present at the beginning of the experiment gradually are lost until the bodies of the organisms become remarkably transparent. For a long time there is no swelling of the body, but rather a narrowing, doubtless due to the loss of the food vacuoles; towards the last there may be a certain amount of swelling but the pellicle very rarely ruptures as it does in various species of *Paramecium*.

5. *Coleps hirtus*. This species forms a marked contrast with the preceding, being the least resistant of all the ciliates studied. Even the most resistant individuals hardly approach the least resistant ones of the other forms. The effect of the carbon dioxide is seen almost instantly. The animals show no decided negative reaction, apparently being overcome too quickly for such to occur. The normal, rather active movements of locomotion cease within a few seconds and thereafter only irregular 'vibrating' movements occur up to the time of death, of which the average is well under five minutes. Even the most resistant individuals do not live for ten minutes. The visible effects of the carbon dioxide are greater on this form than any of the others studied. The barrel-shaped body swells until it is broadly elliptical or even circular in outline, the increase in volume being very decided. At the same time the plates of the armature become indistinct and disappear, giving the appearance at least of actually being dissolved away. In consequence the body becomes very transparent and the protoplasm may be seen to undergo coagulation phenomena. The cilia sometimes beat after the armature has partly or entirely disappeared but usually their movements cease early. The cell in most cases bursts, generally at one of the ends; sometimes this occurs in two or three minutes, before much swelling has taken place.

6. *Blepharisma lateritia*. This on the whole is a very resistant form, being second only to *Colpidium* in this respect. It shows, however, rather more individual variation in the same culture than most of the other forms studied, isolated individuals sometimes succumbing quite early. Strangely enough, in spite of its general resistance its movements are very quickly affected. At

first it exhibits a slight negative response which, however does not last very long and is not so decided as in the case of many of the other forms. Very soon its movements, never very active, become markedly slowed, and for long periods there is either no locomotion at all or this is very slow. The membranelles and cilia, however, keep on beating up to the time of death, which in the majority of cases occurs in from three to six hours. These two structures in *Blepharisma* seem to have about the same resistance. Two phenomena which are particularly characteristic of this species are the marked change in form which occurs and the tendency towards the formation of large vacuoles in the protoplasm. The body, originally lanceolate, within an hour or two often becomes very broadly ovate or sometimes almost circular in outline. Corresponding to the general variability of the species in other respects, there is a great individual variation in this regard also. Towards the end, considerable distortion of the body occurs but bursting is rare.

7. *Euplotes patella*. This form, on account of its peculiar cuirass-like modification of the pellicle might be expected to show a high resistance, but such is not the case. Its resistance in general is somewhat below that of *Paramecium aurelia*. The effect of the carbon dioxide on it becomes apparent very early. It is not markedly stimulated, though it does show a negative response at first. The normal movements of locomotion disappear as a rule after five to ten minutes, although the membranelles sometimes keep on moving an hour longer. However, in most cases the average time of death is considerably less than this—generally under half-an-hour. The cell very early becomes much distorted and the pellicle of the ventral surface ruptures, allowing the escape of drops of clear protoplasm, while the macronucleus at the same time becomes very distinct and granular. Even after these changes have occurred, however, the membranelles continue their beat for a considerable time; the cirri are almost as resistant, though their movements are very irregular and uncoordinated towards the last. The average time required for all movements to cease varied in different experiments from about twenty-five minutes to a little over an hour. Rossbach

('72) claims that not only Euplotes but also Stylonychia and Chilodon and higher animals as well were completely killed by carbon dioxide in three minutes. Such low figures give grounds for the suspicion that his gas was not pure or that some other disturbing factor was present.

8. *Vorticella nebulifera*. This in many respects is the most interesting form studied. It presents a case where both vibratile structures (membranelles) and contractile ones (myonemes of the 'bell' and contractile filament of the stalk) are highly developed, and it is a point of considerable interest to compare the effect of carbon dioxide on these two classes of structures in the same cell. Its effects are as follows. Almost instantly when the gas is turned on the animal is strongly stimulated and makes perhaps half-a-dozen violent contractions of the stalk, which then slowly relaxes, and thereafter so long as the gas is allowed to flow neither contracts spontaneously nor can be made to do so by mechanical stimuli. The time required to produce this paralysis of the stalk varies from thirty to sixty seconds. The myonemes of the 'bell' are similarly affected and the animal remains fully expanded throughout the experiment. If the gas is not allowed to act too long, full and speedy recovery may occur on removal to the air. For instance, in one experiment after a five minutes' exposure to carbon dioxide and a subsequent five minutes' exposure to the air the animals were all normal in every respect. If the exposure to the gas is longer continued, however, permanent injury to the stalk results. After fifteen minutes the animals show a strong tendency to drop off of their stalks and the latter can be seen to be altered in appearance, the contractile filament becoming broken up into irregular refractive fragments and droplets. If the detached animals recover, they regenerate a new stalk.

The effect on the membranelles is almost the reverse of that on the contractile structures. At first they may show a temporary cessation of movement but usually inside a few moments they begin beating again and may continue to do so for three-quarters of an hour or more. Sometimes they stop temporarily and then start again even in the carbon dioxide while, removed to the air,

they show considerable powers of recovery after a lengthy period of rest. In this respect they differ from the membranelles of *Euplotes* and *Blepharisma* which in these experiments never could be made to resume their beat after having completely stopped. Doubtless this difference is due to the fact that in *Vorticella* they are accustomed to stopping every time the disc is retracted, while in the other two forms they normally remain in continuous motion and are stopped by nothing short of actual injury to the cell.

The powers of recovery of *Vorticella* after all movements have ceased are quite considerable. In one experiment after three-quarters of an hour practically all of the individuals had become quiet, and many had been in this condition for half-an-hour or more. Five hours after exposure to the air in a moist chamber about half of them had recovered and many had begun to regenerate the missing stalk, which was already one-tenth to one-half the length of the body. By the next day these stalks were one-half to two times the body length. In this experiment about 50 per cent of the individuals never recovered and this is typical of a number of experiments that were tried. It may be said, therefore, that certain of the movements of *Vorticella* are almost instantly affected and others only after a much longer time. Even after all visible movements have ceased the powers of recovery of the animals are considerable.

In a few instances individuals were observed which, before the beginning of the experiment, had formed the circlet of cilia used in the free-swimming existence. Such cilia were about as resistant as the membranelles, though they were not observed to beat again after having stopped. In no case did individuals which broke from their stalks during the course of the experiment on account of the effect of the carbon dioxide, form such cilia, but their locomotion was entirely by means of their membranelles.

The *Vorticella* cell apparently shows no tendency to burst and form droplets of protoplasm, but a considerable change in form may occur. In an atmosphere of carbon dioxide *V. nebulifera* inside a few minutes tends to assume the more rounded form characteristic of *V. campanula*. In the individuals which are

killed the protoplasm becomes brownish and opaque, doubtless due to coagulation phenomena.

### *B. Flagellates*

1. *Peranema trichophorum*. This form shows conditions which suggest those already noted in *Vorticella*. As is well known, *Peranema* has a single very prominent flagellum, which in locomotion is directed straight forward. Ordinarily it is quite rigid except the tip, whose movements cause a slow forward progression of the animal. During progression, and also when otherwise at rest, the body shows very decided changes in form, these 'metabolic' movements, or contortions, being one of the most striking characteristics of the species. When exposed to carbon dioxide *Peranema* responds perhaps as quickly as any of the forms studied. Its forward progression ceases almost instantly and after a few preliminary, and rather vigorous contortions, the body suddenly becomes paralyzed in whatever state of contraction it may happen to be in at the time. Only rarely does the animal have time to contract to a spherical form before being overtaken with this paralysis; consequently the typical appearance of the body is an irregular mass which does not change its form so long as the stream of carbon dioxide is allowed to flow.

The flagellum responds differently. Contact with the carbon dioxide causes it to beat with a swinging motion in which the proximal as well as the distal portion is concerned. Sometimes these movements are rather vigorous, but they never give rise to locomotion. They may continue with more or less uniformity for a half or even three-quarters of an hour; at the end of that time the flagellum gradually comes to rest. All visible movements have now ceased, but the animals are not necessarily dead. Experiments were tried to determine what powers of recovery *Peranema* possesses after becoming perfectly motionless. It was found that when the drop containing them is removed from the gas chamber and placed in contact with the air, a considerable percentage of the individuals may recover after an exposure of an hour and a quarter to carbon dioxide, even though all movements have for a

long time ceased. In the case of individuals exposed for two hours, however, no recoveries occurred although the drop was kept under observation for twenty-four hours. The time required for recovery to occur depends on the length of time the gas has acted. After an exposure of five minutes, metabolic movements of the body begin in less than a half minute after contact with the air, and the animals may be entirely normal in ten minutes. After a longer exposure the time required is much greater. In one experiment after an exposure of thirty-four minutes, but few of the animals were in a state of normal activity after an hour-and-a-half in the air, though at the end of four hours most of them showed no signs of injury and were normal in every respect.

*Peranema* therefore represents a form in which the effects of carbon dioxide on locomotion and the contractile movements of the body are almost instantaneous, but which is killed only after a prolonged exposure. The point of greatest interest is that while certain movements of the body are brought to a standstill in a few seconds the flagellum may continue to beat for half-an-hour or more. We are therefore dealing with structures concerned in producing movements in the same cell which show a considerable physiological difference.

2. *Euglena viridis*(?). This form is in some respects more resistant and in others less resistant than *Peranema*. The time required for locomotion to cease is longer and the powers of recovery after an extended exposure greater, but the flagellum is much more sensitive and the length of time required to bring to an end all visible movements is considerably less. Like *Peranema*, *Euglena* shows no decided negative reaction to the gas as do many of the forms studied, though locomotion may persist for a few moments. Often the first effect of the gas is to cause a short temporary cessation of all movements, which quickly reappear. Soon, however, movements of progression cease and the organisms show signs of life only by vibrating movements which are due to the abnormal beat of the flagellum. These gradually cease and the animals sink to the bottom of the drop motionless and perfectly extended. The time required to produce cessation of all movement varies from two or three to ten minutes. The



particular *Euglena* studied, which was close to, but probably not identical with, *E. viridis*, was not one which very actively changes its form, and consequently was not a very favorable one in which to observe the effect of carbon dioxide on the contractile movements of the body. It may be said, however, that while 'euglenoid' movements were observed in many individuals before the beginning of the experiment and also after recovery, they never occurred during its progress, consequently the conditions here probably are the same, even if less striking, than those found in *Peranema*.

After the organisms have settled to the bottom of the drop and become motionless the only change that can be observed is a gradual slow swelling of the body. At the same time there is a slight shortening which, however, is not sufficient to account for the greater thickness of the organisms as careful measurements show. This swelling continues until the shape of the body has changed from cylindrical to broadly elliptical in outline and the chlorophyll bodies appear forced apart from each other. In extreme cases the cell may appear to be at the point of rupture, though this rarely occurs, the pellicle being very tough and elastic.

Although all movements cease in *Euglena* in ten minutes or less, it requires a much longer time to kill the organisms. Even after an exposure of three hours about a third of the individuals eventually recovered, though the time required was considerable. The recovery of *Euglena* is far slower than that of *Peranema*. After an exposure of seven minutes no recoveries could be noticed a half hour after removal to the air, although they began to occur soon after that, and in an hour and a quarter practically all the individuals were normal. After an exposure of two or three hours, the time required for recovery is three or four hours or more.

3. *Chilomonas paramecium*. This form shows great individual and also cultural variation. While in a few cases the animals become motionless in fifteen or twenty minutes, the average time required generally is three-quarters of an hour or more. Many resistant individuals retain their movements for several hours. In general, therefore, this may be said to be a form with a high resistance. Unlike the two previous flagellates, *Chilomonas*

shows most decided reactions to the presence of carbon dioxide. The first effect is often to cause a temporary cessation of motion which lasts however only for a few seconds, after which the animals are remarkably active. They show a striking tendency to seek the center of the drop at first, later becoming uniformly distributed again. Their motions at first are normal but gradually the animals come to rest and give evidences of life only by a slow rotation or by quick darting movements which they occasionally make. In practically every case the cell becomes circular in outline and if the experiment be long continued may actually burst. *Chilomonas* like the preceding form also has considerable powers of recovery after all motion has ceased. In one experiment even after an exposure to carbon dioxide of two-and-a-half hours about 75 per cent of the individuals eventually recovered after exposure to the air. In other cases, however, even after a shorter exposure the mortality is greater.

4. *Entosiphon sulcatum*. This form unfortunately was studied in only one experiment in which, however, a considerable number of individuals was present. Judging from these rather incomplete data, it is by far the most resistant of the flagellates examined. After an exposure of five hours it not only was alive, but the movements were not very markedly affected. Both flagella continued to beat, though in rather a stiff and jerky fashion, and slow forward progression continued. How long it would have survived cannot be said, but probably the time would have been considerably above that mentioned, since when the experiment had to be ended none of the animals had as yet been killed.

#### IV. DISCUSSION OF RESULTS

From the results given it is apparent that all of the forms studied are injured and eventually killed by pure carbon dioxide, but that the resistance of the different forms is very different. *Colpidium colpoda* can withstand without injury an exposure of many hours, while *Coleps hirtus* is killed in three or four minutes. Sometimes the time of cessation of visible movements and the point at which the cell is so severely injured that recovery cannot occur, may coincide, as in most of the ciliates (in *Euplotes patella*

irreparable injury probably occurs before the membranelles cease beating) while in other cases, the animal is capable of full recovery long after all movements have ceased, e.g., flagellates and Vorticella. Some animals which are otherwise fairly resistant to carbon dioxide, as shown by their powers of recovery after a protracted exposure to it, or by the long continuation of visible movements, show its effects very quickly by their inability to carry on normal locomotion in its presence. *Paramecium* is the most striking example of this condition, *Euglena* and *Euplotes* also being relatively quickly affected. In their primary response the different forms also show distinct differences. The three species of *Paramecium* studied as well as *Colpidium*, and *Chilomonas* show a decided negative reaction and an effort to escape from it. This reaction is less marked in *Blepharisma* and *Euplotes*, while in the other forms it is practically lacking, probably because normal movements are so quickly interfered with. (*Entosiphon* was not studied in this connection.) It will be seen, therefore, that the different forms studied show certain characteristic differences in reactions and general resistance to carbon dioxide.

It has already been pointed out that there is a certain amount of individual and cultural variation in the same species, which makes it impossible to put in exact quantitative form the time in which death occurs, etc. Nevertheless the relative resistance of each form as compared with other forms from the same culture is fairly constant and furthermore it is at least possible to say that certain forms always have a high, and others always a low resistance. While some forms may 'overlap,' others, as for example *Colpidium* and *Coleps*, never do.

The observations here recorded are not the first that have been made on the differences in resistance to carbon dioxide shown by different organisms. Fränkel ('88) studied the effect of this substance on various bacteria with the result that some were found to thrive almost as well as in air, others had their development checked but were not killed, while others were quickly destroyed. Lopriore ('95) also, in his careful experiments on the effects of carbon dioxide on the spores and mycelia of fungi and the pollen

tubes of angiosperms, found decided specific differences. Many other scattered observations exist, which however, it is difficult to compare on account of the different methods employed in obtaining them.

It is interesting to consider the results here obtained in connection with those of Jennings and Moore ('01) on the chemotactic effect of carbon dioxide on various protozoa. Of the four forms mentioned by them as being attracted by this substance, three (i.e., *Paramecium caudatum*, *Colpidium colpoda*, and *Chilomonas paramecium*) have been studied in these experiments and all show marked powers of resistance, as well as a strong negative response when the concentration is suddenly made high in the edges of the drop. Of the forms found by them to be indifferent, unfortunately only two genera (*Euglena* and *Euplotes*) were available, but these both showed a relatively low resistance as compared with related forms, at least so far as the continuance of locomotion is concerned. It would be interesting to study the other members of their list in this connection. Doubtless many other facts of behavior could be brought into line with such physiological peculiarities as the one under consideration.

One of the most interesting results that appears from these experiments is the striking difference that seems to exist between the contractile elements of the cell—the myonemes—on the one hand, and the vibratile ones—cilia, membranelles, and flagella on the other. The former are very quickly thrown out of function while the latter continue their normal movements for a long time. The best illustration of this point is *Vorticella*, in which the contractile filament of the stalk, and the myonemes, after a primary stimulation, are inside a minute or less completely paralyzed, while the membranelles perhaps after stopping for a short time continue to beat for three-quarters of an hour. Such results are in agreement with those obtained by other workers. Neresheimer ('03), for example, found that the myonemes and membranelles of *Stentor* are differently affected by substances like morphin, which paralyze the former and do not affect the latter. Lillie ('12) has observed that the cilia of *Arenicola* larvae continue their activity for hours in isotonic sugar or magnesium chloride

solutions, or in solutions of chloroform or ether, which prevent completely all muscular movements. Recently Mayer ('11) has found that the effects of many ions on ciliary and muscular movements are exactly opposite those that depress the one stimulating the other. He found that the ciliary movements of trochophore larvae at first cease in water charged with carbon dioxide but later start again. It is well known that carbon dioxide at first stimulates and later depresses muscular movements in the higher vertebrates (Lee, '07). In *Vorticella* in the same cell this antagonistic action appears very clearly. In other forms it is harder to demonstrate a primary depression of ciliary activity, possibly because of the response of the organism as a whole in an adaptive way. In *Chilomonas*, however, the primary depression of the movements of the flagella nearly always occurs.

#### V. SUMMARY

1. Each of the twelve forms studied reacts to carbon dioxide in a characteristic way and has a characteristic resistance, which is highest in *Colpidium colpoda*, which remains alive many hours, and lowest in *Coleps hirtus*, which is killed in a few minutes. A certain amount of individual and cultural variation may occur which prevents the expression of the resistance of the species in absolute terms. Compared with other forms under the same conditions, however, the relative resistance is fairly constant.

2. Some forms are killed outright very quickly (*Coleps hirtus* and *Paramecium bursaria*). In others all movements are stopped in a few minutes but death occurs relatively late, the powers of recovery being high (*Euglena*). In still others, locomotion ceases very promptly but movements of the cilia, flagella, etc., may persist for a long time (*Peranema trichophorum*, *Euplotes patella*, etc.). In the remainder, more or less normal locomotion continues for a considerable time (most of the ciliates, *Chilomonas* and *Entosiphon*). The result in all cases, however, if the experiment be long enough continued, is cessation of movements and death.

3. In the same cell the contractile elements are usually quickly paralyzed (*Vorticella* and *Peranema*) while the vibratile structures (cilia, membranelles, flagella) are much more resistant. In some

cases (*Vorticella*) the action of carbon dioxide on these two classes of structures is exactly opposite, the contractile elements being first stimulated and then paralyzed and the vibratile ones often temporarily stopped and then started again.

4. Ordinary cilia and their modifications, membranelles and cirri when present in the same cell show approximately the same resistance. Flagella show great variation, that of *Euglena* being paralyzed in a few minutes and those of *Chilomonas* and *Entosiphon* remaining active for several hours.

5. In ciliates in general, with the exception of the specialized *Vorticella*, recovery after complete cessation of movement is impossible; in the flagellates, movement ceases long before the cell is permanently injured.

6. The general effects of carbon dioxide on the cell are to cause (a) cessation of movement, (b) absorption of water and consequent swelling, (c) injury to the cell wall, (d) death and coagulation of the protoplasm.

#### BIBLIOGRAPHY

- BUDGETT, S. P. 1898 On the similarity of structural changes produced by lack of oxygen and certain poisons. *Am. Jour. Physiol.*, vol. 1, pp. 210-214.
- FRÄNKEL, C. 1888 Einwirkung der  $\text{CO}_2$  auf die Lebenstätigkeit der Mikroorganismen, *Zeitschr. f. Hygiene*, vol. 5, pp. 332-362.
- JENNINGS H. S. and MOORE, E. M. 1901 Studies on reactions to stimuli in unicellular organisms. VIII. On the reactions of Infusoria to carbonic and other acids with especial reference to the causes of the gatherings spontaneously formed. *Am. Jour. Physiol.*, vol. 6, pp. 233-250.
- LEE, F. S. 1907 The action of normal fatigue substances on muscle. *Am. Journ. Physiol.*, vol. 20, pp. 170-179.
- LILLIE, R. S. 1912 Antagonism between salts and anaesthetics. *Amer. Jour. Physiol.*, vol. 29, pp. 372-397.
- LOEB, J. and HARDESTY, I. 1895 Ueber die Localization der Athmung in der Zelle. *Pflüg. Arch.*, vol. 61, pp. 583-594.
- LOPRIORE, G. 1895 Ueber die Einwirkung der Kohlensäure auf das Protoplasma der lebenden Pflanzenzelle *Jahrb. wiss. Bot.*, vol. 28, pp. 531-626.
- MAYER, A. G. 1911 The converse relation between ciliary and neromuscular movements. *Papers from the Tortugas Laboratory of the Carnegie Institution of Washington*, vol. 3.

- NERESHEIMER, E. 1903 Ueber die Höhe histologischer Differenzierung bei heterotrichen Ciliaten. Arch. f. Protistenkunde, vol. 2, pp. 305-325.
- PROWAZEK, S. von 1903 Studien zur Biologie der Zelle. Zeitschr. f. Allg. Phys., Bd. 2.
- ROSSBACH, M. J. 1872 Die rhythmischen Bewegungserscheinungen der einfachsten Organismen und ihr Verhalten gegen physikalische Agentien und Arzneimittel. Verh. d. phys. med. Gesell. zu Würzburg, N. F., vol. 11, pp. 179-242.

CERTAIN MEANS BY WHICH STARFISH EGGS NATURALLY RESISTANT TO FERTILIZATION MAY BE RENDERED NORMAL AND THE PHYSIOLOGICAL CONDITIONS OF THIS ACTION.

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Last summer at Woods Hole, while investigating the influence of ether and other anæsthetics in protecting the unfertilized eggs of starfish against the cytolytic action of pure isotonic sodium chloride solution,<sup>1</sup> I observed that toward the end of the breeding season the eggs often proved abnormally resistant to this solution, withstanding in some instances exposure of more than three hours to 0.55*m* NaCl without losing the power of development on fertilization; in normal eggs this solution typically causes complete cytolysis and coagulation of the protoplasm in two hours or less. Other characteristic abnormalities of behavior were found to be associated with this abnormal resistance to salt solutions. Usually a large proportion of such eggs failed to undergo maturation in sea-water, and of those which matured only a small proportion developed to a free swimming stage on fertilization, and the resulting larvæ were largely abnormal. Also the mature eggs, if left unfertilized in sea-water, frequently failed to die and break down within the usual time, but remained clear and apparently normal in appearance for an unusually prolonged period. It is well known that unfertilized mature starfish eggs undergo spontaneously a characteristic cytolytic alteration, accompanied by a darkening or coagulation of the protoplasm, which is typically complete within twelve to fifteen hours after deposition;<sup>2</sup> in contrast to this behavior a considerable proportion of the eggs under consideration often remained clear and uncoagulated in sea-water for twenty-four and in some cases for forty-eight hours. These several peculiarities, (1) failure of

<sup>1</sup> *American Journal of Physiology*, 1912, Vol. 30, p. 1.

<sup>2</sup> Cf. J. Loeb, *Archiv für die gesammte Physiologie*, 1902, Vol. 93, p. 59.



maturation in a large proportion of eggs, (2) failure of those eggs which did mature to develop after fertilization, (3) marked delay in the typical post-maturational cytolysis of unfertilized eggs, and (4) unusual resistance to the cytolytic action of salt solutions were found in more or less constant association with one another in numerous lots of eggs. All of these peculiarities are evidence of a certain inertia or resistance to change in the egg-system; such eggs fail to react, or react slowly and imperfectly to conditions which call forth a definite and regular response in normal eggs. The fact of their concurrence, as well as their general nature, suggests that some single structural or metabolic abnormality, whose general effect is to lower reaction-velocities in the egg-system, is responsible for all of these peculiarities of behavior.

The further incidental observation was made in several instances that such eggs after treatment for two or three hours with sodium chloride solution containing a little ether or chloral hydrate recovered to a considerable degree the power of developing to a normal larval stage on fertilization; *i. e.*, eggs so treated yielded more numerous and more active larvæ than the untreated eggs of the same lot, fertilized at the same time. Pure sodium chloride solution showed a similar though less marked action. The surprising result thus appeared that treatment with solutions which are markedly injurious to normal eggs may bring a certain proportion of these abnormal or "over-ripe" eggs into a condition—as regards power of development on fertilization—closely approaching the normal.

The following record will illustrate the above-described conditions in detail.

June 29, 1911. The eggs were removed from a considerable number of starfish at 10.00 A.M. A large proportion of these mixed eggs remained permanently immature in sea-water (with intact germinal vesicles), but about half underwent apparently normal maturation. On fertilization (at 3:30 P.M.) very few of the eggs—a fraction of one per cent.—formed blastulæ, most died in early cleavage stages, but many failed to cleave or even to form fertilization-membranes. The unfertilized mature eggs after twenty-four hours in sea-water remained for the most part clear and translucent with no sign of coagulation; a good many, however, showed apparently normal coagulation, while others showed an intermediate condition. After forty-eight hours many unfertilized mature eggs were still uncoagulated.

About two hours after removal from the animals the unfertilized eggs were

placed in the following solutions: (1) pure 0.55*m* NaCl, and (2-10) 0.55*m* NaCl containing anæsthetics as follows: (2-4) ether, 0.6, 0.45, and 0.3 volumes per cent., (5-7) chloral hydrate, 0.6, 0.4 and 0.2 per cent., (8-9) chloroform, one sixth and one tenth saturated, and (10) ethyl alcohol, 5 volumes per cent. After three hours and fifteen minutes in these solutions the eggs were transferred to normal sea-water and washed free of the anæsthetics by two changes of sea-water; spermatozoa were then added. At the same time spermatozoa were added to the untreated eggs which had remained in sea-water. The results were as follows: of the control eggs, fertilized in sea-water without treatment, almost all died before reaching the blastula stage; only a few feeble blastulæ (a fraction of 1 per cent.) were found on careful search; many eggs failed to cleave or even to form membranes. The eggs exposed to pure 0.55*m* NaCl also formed few blastulæ, but these were relatively somewhat more numerous as well as more active than in the control; the eggs treated with 0.55*m* NaCl containing 0.45 and 0.3 vol. per cent. ether, especially the latter, showed a more decided improvement over the control, though the proportion of blastulæ was still small. The eggs from the other solutions showed no improvement.

A similar result was observed in a second series of experiments with eggs which showed similar peculiarities. Eggs treated for three hours with 0.55*m* NaCl containing 0.3 vol. per cent. ether gave about 5 per cent. of blastulæ, while of the control untreated eggs less than one per cent. reached this stage. Eggs similarly treated with solutions containing a higher proportion of ether (0.75, 0.6, and 0.45 vol. per cent.) showed no improvement over the control. In another series eggs exposed for 3 h. 45 m. to 0.55*m* NaCl containing 0.1 per cent. chloral hydrate gave considerably more blastulæ than the control eggs.

It is to be noted that the improvement in the developmental power of these abnormal or resistant eggs was produced only by the pure salt solution or by solutions with a *low* concentration of anæsthetic. The concentration of ether most favorable for retarding the cytolytic action of 0.55*m* NaCl is considerably higher—from 0.5 to 0.6 vol. per cent.<sup>1</sup> The present effect, however, is not due to a simple prevention of cytolysis; the improvement over eggs left in sea-water, none of which undergo cytolysis within the time of exposure, cannot thus be explained. The effect is different from a simply protective action; and since it seemed to be favored by weak solutions of ether, the experiment was tried of exposing a batch of similarly abnormal eggs to sea-water containing 0.3 vol. per cent. ether. After three hours the eggs were returned to normal sea-water and fertilized. Next day it was found that the great majority of mature eggs had formed

<sup>1</sup> Cf. R. S. Lillie, *loc. cit.*, p. 6.

active and vigorous blastulæ and gastrulæ, while of the untreated control eggs left in sea-water and fertilized at the same time as the others less than one per cent. formed larvæ and these were feeble and abnormal. It thus appeared that the abnormal condition which renders the egg incapable of responding fully to the fertilizing action of the spermatozoön might be removed by treatment with sea-water containing ether in certain concentrations, which are considerably lower than those required for typical anæsthetic or protective action.

What are the conditions of this effect? In a recent paper<sup>1</sup> I have presented evidence indicating that the protective and anæsthetic actions exerted by ether and other lipid-solvents in certain concentrations are due primarily to a *modification of the plasma membranes* of the cells or irritable elements, of such a kind as to render these membranes more resistant toward agencies that under the usual conditions rapidly increase their permeability; cytolysis and stimulation, both of which depend on such increase of permeability, are hence checked or prevented. Decrease in the readiness with which the permeability is increased thus involves for an irritable tissue decreased irritability; this effect is produced by various salts, *e. g.*, of magnesium, and by ether and other lipid-solvent anæsthetics in certain (not too high) concentrations. In lower concentrations it has been observed that ether and other lipid-solvents frequently *heighten* irritability;<sup>2</sup> *i. e.*, expressed in terms of the membrane theory of stimulation, they increase the readiness with which the permeability—and hence the electrical polarization—of the plasma membrane undergoes change. It seems clear that for irritable tissues the state of the lipoids in the plasma membrane largely determines the readiness with which changes of permeability—and of the dependent electrical polarization—are induced by external agencies. Slight permeation of the lipoids with a lipid-solvent like ether apparently often facilitates such changes and hence in-

<sup>1</sup> R. S. Lillie, *American Journal of Physiology*, 1912, Vol. 29, p. 372.

<sup>2</sup> For various instances of this effect cf. the references cited in my recent paper in *American Journal of Physiology*, 1912, Vol. 29, p. 374. The neuromuscular system of marine animals also shows it; *e. g.*, Bethe found that alcohol (0.5 per cent. in sea-water) decidedly increased the mechanical irritability of the isolated central portion of the medusa *Cotylorhiza*; cf. "Allgemeine Anatomie und Physiologie des Nervensystems," Leipzig, 1903, p. 359.

creases irritability; the presence of more lipid-solvent renders a change of permeability difficult,<sup>1</sup> hence the protective or anæsthetic action; while concentrated solutions of lipid-solvents disrupt the membrane and produce cytolytic or irreversible alterations in the cells; hence such substances in higher concentrations are markedly toxic.

On the assumption that lipid-solvents influence the plasma membranes of egg cells in essentially the same manner as those of irritable tissues, the above action of ether on abnormal egg cells becomes more readily intelligible; it falls, in fact, into the same essential category with the facts just cited. There is a close analogy between the stimulation of irritable tissues and the initiation of cleavage in egg cells; the primary or critical change in both cases appears to be a temporary and reversible increase in the permeability of the plasma membrane, with accompanying changes in the electrical polarization of the latter.<sup>2</sup> This analogy suggests that the irresponsive condition of the above "over-ripe" starfish eggs is essentially the symptom or expression of an abnormal condition of the plasma membrane. Apparently the latter has in these eggs become *abnormally resistant to changes of permeability*; hence the eggs are irresponsive to the spermatozoön (whose primary action is to increase permeability); hence also they show heightened resistance to cytolytic action—which also depends on increase in surface permeability; this is shown by the slowness with which they undergo the typical post-maturational cytolysis, and also by their increased resistance to pure isotonic sodium chloride solution. If this interpretation is correct, the favorable action of weak ether solution consists essentially in altering the plasma membrane and rendering it more susceptible to the action of permeability-increasing (and hence depolarizing) agencies—*i. e., more irritable*, on the above-mentioned analogy with irritable tissues. Through this means the plasma membrane is restored to an approximately normal condi-

<sup>1</sup> This is very clearly shown in the larvæ of *Arenicola*; cf. the paper just cited, p. 380 ff.

<sup>2</sup> I have discussed the probable basis of this resemblance at some length in an earlier paper in the BIOLOGICAL BULLETIN, 1909, Vol. 17, pp. 20 ff. The title of Loeb's recent book, "Entwicklungserregung des tierischen Eies," also emphasizes this analogy.

tion of responsiveness; the sperm then exhibits its normal action. It is evident that this hypothesis also implies that the other changes in the egg expressive of increased permeability should, after the ether treatment, also follow an approximately normal course. This in fact the case as regards the post-maturational cytolysis; this change is delayed in the above abnormal eggs, as already described; but it is found to take place in a normal manner in the ether-treated unfertilized eggs. The following descriptions will illustrate both of these effects.

It should first be noted that the degree to which eggs abnormally resistant to fertilization may be rendered normal by the ether treatment is variable. In some of my last summer's experiments the difference between the ether-treated and the untreated eggs of the same lot was slight; in others the contrast was most striking. The degree of resistance to the post-maturational cytolysis is similarly variable. In general it was observed that eggs which showed the most pronounced delay in the onset of this latter change were most readily brought into a normally responsive condition—or "rejuvenated"—by ether. The following series of experiments with three separate lots of starfish eggs—all of which failed with a few exceptions to develop to a blastula stage on simple fertilization without ether treatment—illustrates this variability, as well as the correlation between delay in the post-maturational cytolysis and the possibility of rejuvenation<sup>1</sup> by the ether treatment.

June 30, 1911. Three separate lots of eggs (A, B, C) were used; each lot consisted of the mixed eggs from several starfish. After remaining about one and a half hours in normal sea-water, eggs from each lot were transferred to sea-water containing 0.3 vol. per cent. ether. These eggs were kept in small tightly corked flasks. After 1 hour and 10 minutes in this solution part of the eggs were transferred from each flask to normal sea-water in finger bowls; after washing the eggs free from ether spermatozoa were added. The remainder of the eggs in each flask were similarly transferred to sea-water and fertilized after three and a quarter hours in the ether solution. For each lot there was a *fertilized control* consisting of eggs which had lain untreated in sea-water for about 2 hours and 45 minutes before fertilization.

<sup>1</sup> I use this term because of the analogies it suggests. The eggs are in fact brought by the ether treatment into a condition which is characteristic of eggs produced in the earlier portion of the reproductive cycle. The production of hyper-resistant eggs like the above occurs late in the breeding season, and the phenomenon bears certain analogies to senescence. See below, page 345.

The characteristics and behavior of the eggs from these three lots were respectively as follows:

LOT A.—The great majority of these eggs fail to mature. A small proportion undergo apparently normal maturation.

*Unfertilized Eggs.*—22 hours after removal almost all of the mature eggs show the typical opaque and coagulated protoplasm; i. e., post-maturational cytolysis appears normal.

*Fertilized Eggs.*—Condition ca. 20 hours after fertilization.

1. *Untreated (Control) Eggs.*—Many of the immature eggs have typical fertilization membranes; but are otherwise unchanged. The few mature eggs are mostly dead; only one abnormal blastula was found.

2. *Ether-treated Eggs.*—(a) Exposed 1 hour 10 minutes. Four or five blastulæ are found in some hundred eggs; little difference from control. (b) Exposed  $3\frac{1}{4}$  hours. Little or no improvement over control; a few blastulæ as in (a).

LOT B.—Most of these eggs remain immature, but about 20 per cent. undergo apparently normal maturation.

*Unfertilized Eggs.*—22 hours after removal from the animals most of the mature eggs are opaque and coagulated, but in many the coagulation is less advanced than in normal eggs, and in some the protoplasm remains semi-translucent.

*Fertilized Eggs.*—Condition ca. 20 hours after fertilization.

1. *Untreated (Control) Eggs.*—Almost all of the mature eggs are dead. Many immature eggs have fertilization membranes. Only two abnormal blastulæ are found in several hundred eggs.

2. *Ether-treated Eggs.*—(a) Exposed 1 hour 10 minutes. Improvement over the control; a large proportion (about one third) of the mature eggs have formed blastulæ, many of which have begun to gastrulate. (b) Exposed  $3\frac{1}{4}$  hours. Also shows a marked improvement over the control, but the larvæ are fewer and less active than in 2a.

LOT C.—In this lot of eggs the majority show normal maturation, though a few remain immature.

*Unfertilized Eggs.*—After 22 hours in sea-water most of the eggs are more or less coagulated, but the degree of opacity is distinctly less than in normal eggs, and a considerable proportion remain translucent—almost like freshly shed eggs.

*Fertilized Eggs.*—Condition ca. 20 hours after fertilization.

1. *Untreated (Control) Eggs.*—Nearly all are dead. Most have membranes and show evidence of having cleaved or fragmented, but many have failed to cleave or even to form membranes. A small proportion of eggs have formed larvæ some of which appear normal: the larvæ though few are more numerous than in the controls of A and B.

2. *Ether-treated Eggs.*—(a) Exposed 1 hour 10 minutes. Striking contrast to control. Almost all of the mature eggs have formed active larvæ, many in the early gastrula stage and swimming at the surface of the water. (b) Exposed  $3\frac{1}{4}$  hours. Here also the majority of eggs form larvæ, but these are largely abnormal, and relatively few gastrulæ or surface swimmers are present.

The power of development after fertilization is thus greatly increased after ether-treatment in Lots B and C, but not in Lot A. The mature eggs of Lots B and C show marked delay in the post-maturational cytolysis; in Lot C this delay is greater, and the

action of the ether is correspondingly more favorable, than in Lot B. I have already presented evidence that eggs showing this abnormal behavior are characterized by the possession of hyper-resistant plasma membranes. It should be noted that variations in the degree of resistance of this membrane occur regularly in normal eggs. Various facts indicate that the process of maturation is constantly associated with a change in the properties of the plasma membrane. This is shown by the fact that mature eggs undergo cytolysis in 0.55*m* NaCl solution more rapidly than immature eggs;<sup>1</sup> also by the fact that contact with spermatozoa and various forms of artificial treatment cause the separation of the surface-film of mature eggs in the form of a fertilization membrane, a change indicating a superficial cytolytic or permeability-increasing action; while immature eggs are not normally subject to this change.<sup>2</sup> This difference between immature and mature eggs is a constant or physiological feature in the life history of these eggs. The difference between normal eggs and the resistant eggs under consideration is in many respects similar. For some reason the maturation process fails to bring these eggs into the normally sensitive condition in which the permeability of the membrane is readily increased. Hence fertilization is imperfect, even fertilization-membranes failing to form in some cases; in others membranes are formed and cleavage begins, but the latter is characteristically irregular and fails to proceed far. According to this view the failure of development is due not to defective organization of the protoplasm, but simply to the existence of an abnormally resistant plasma membrane. The action of ether consists in restoring the membrane to its normal condition. The response to the spermatozoön then becomes normal.

The experimental evidence in favor of this hypothesis consists at present simply in the fact that such abnormal eggs are rendered normal by ether treatment not only in regard to their response to fertilization, but also in regard to the rate and character of

<sup>1</sup> R. S. Lillie, *American Journal of Physiology*, 1912, Vol. 30.

<sup>2</sup> Cf. J. Loeb's experiments on the eggs of *Asterina*, University of California Publications, *Physiology*, 1905, Vol. 2, p. 150. Spermatozoa and artificial membrane-forming agencies may however produce typical membranes in abnormal immature starfish eggs. Cf. *Journal of Experimental Zoölogy*, 1908, Vol. 5, p. 407.

the spontaneous post-maturational cytolysis; *i. e.*, they undergo complete coagulation within eighteen hours or less, precisely as do normal eggs. Whether the resistance to cytolysis by salt solutions is also decreased I have not yet determined; but the decrease in the resistance to the post-maturational cytolysis—a change supposedly due to the action of certain protoplasmic oxidation products upon the plasma membrane<sup>1</sup>—is clear evidence that the membrane has been brought into a condition more nearly approaching the normal. The experiments to be described show that a return of the normal responsiveness to the spermatozoon is closely correlated with a return of the normal behavior with respect to this spontaneous oxidative cytolysis. In other words, the plasma membranes of the ether-treated “rejuvenated” eggs undergo breakdown in the manner and at the time characteristic of normal eggs.

The following record gives the description of two typical experiments.

July 6, 1911. Eggs were removed at 11:00 A.M. from two lots of starfish, *A* and *B*. In both lots a good proportion of eggs underwent apparently normal maturation. Eggs from each lot were divided into two portions. One portion remained in sea-water; and about four hours after removal from the animals part of these eggs were fertilized; the rest remained unfertilized. The other portion was transferred, two hours after removal, to sea-water containing 0.3 vol. per cent. ether; in this solution they remained for one hour and thirty-five minutes; they were then returned to sea-water; to part of these eggs spermatozoa were added, the rest remained unfertilized. The ether-treated and the untreated eggs were fertilized at the same time. The two lots *A* and *B* were treated alike so far as possible. The results of these experiments were as follows:

LOT *A*. The following was the condition of the eggs *ca.* 22 hours after removal:

1. *Untreated Eggs.* (a) *Unfertilized.*—Most mature eggs are coagulated but to a varying degree; some are only slightly darkened, and in a fair proportion the protoplasm remains semi-translucent.

(b) *Fertilized.*—All of the mature eggs have formed membranes and most have undergone cleavage or irregular fragmentation; but many remain uncleaved; no blastulæ are present.

2. *Ether-treated Eggs.*—(In 0.3 vol. per cent. ether from 1.00 to 2.35 P.M.)

(a) *Unfertilized.*—All mature eggs are completely and uniformly coagulated; there are no partly coagulated or semi-translucent eggs.

(b) *Fertilized.*—Decided contrast to 1b. Most eggs are dead, but among these there are no uncleaved eggs; numerous blastulæ and gastrulæ are present, many swimming at the surface.

LOT *B*.—(The condition of the eggs *ca.* 22 hours after removal.)

<sup>1</sup> Since the change is greatly retarded in oxygen-free or cyanide-containing sea-water. Cf. J. Loeb, *Archiv für die gesammte Physiologie*, 1902, *loc. cit.*



1. *Untreated eggs.*—(a) *Unfertilized.*—The degree of post-maturation coagulation varies here as in Lot A, but a larger proportion of eggs remain semi-translucent, and many are virtually unchanged in appearance.

(b) *Fertilized.*—Most eggs have formed membranes and cleaved or fragmented; a number form membranes but fail to cleave. A few feeble blastulæ are present—a fraction of 1 per cent.; no surface swimmers.

2. *Ether-treated eggs.*—(In 0.3 vol. per cent. ether from 1.00 to 2.35 P.M.)

(a) *Unfertilized.*—Marked contrast to 1a. All mature eggs are completely coagulated—opaque, compact looking, without membranes.

(b) *Fertilized.*—A large number of active blastulæ and gastrulæ are present, many swimming at the surface. No uncleaved eggs are present, though a good many have died in early stages. More favorable than A, 2 (b).

The return of the normal responsiveness to fertilization and normal power of development is thus associated with a return of the normal rate of post-maturation cytolysis. This observation was made in six out of nine experiments, at different times and with different lots of eggs, in which ether-treatment led to marked increase in the proportion of eggs undergoing favorable development. In three of the earlier experiments the behavior of the ether-treated unfertilized eggs was not observed; but in all of the six cases where both observations were made concurrently this correlation held. As already mentioned, the degree of improvement effected by the ether has been variable, in correspondence with the degree of abnormality in the eggs. In all of the cases in which the improvement was decided, as in some of those described above, the untreated mature eggs proved largely refractory toward both cytolysis and fertilization; while after the treatment with ether the eggs showed in both respects a behavior approaching the normal. In three other lots of abnormal eggs treatment with ether had no appreciable effect either in accelerating cytolysis or in increasing the proportion of favorably developing eggs; while in one case in which a considerable proportion of untreated eggs developed favorably—about one third forming larvæ—the ether-treated eggs were somewhat *less* favorable than the untreated; in this series the unfertilized eggs, both treated and untreated, showed an apparently normal spontaneous cytolysis. Probably the plasma membranes of these eggs were over-susceptible rather than under-susceptible to increase of permeability. The possible existence of both kinds of abnormalities must be recognized.

Deviation in either direction from the physiological norm would presumably impair the power of development.

#### GENERAL DISCUSSION.

I shall now discuss somewhat more fully the general physiological significance of the above abnormalities and their relations to analogous conditions elsewhere. The above condition, described in general terms, is essentially one of lowered susceptibility to agencies which ordinarily call forth a definite response. Similar conditions exist in other cells and tissues. There are also cases where a tissue is normally irresponsive to certain agencies or conditions, to which however it may be rendered responsive by certain forms of artificial treatment.<sup>1</sup> It seems probable that in all of these cases the condition of the plasma membrane is the essential factor which determines whether the cell or tissue responds to the agency in question or not. This structure, as the most external layer of the cell, is the part most accessible to artificial modification; and if its condition of permeability and electrical polarization plays the controlling rôle in cell-processes which modern investigation tends more and more to indicate, knowledge of the means by which its properties may be altered at will becomes a matter of the highest importance for both the theoretical and the practical aspects of biology.

The abnormalities under consideration appear typically in the eggs of *Asterias forbesii* toward the close of the breeding season. Eggs are abundant at Woods Hole in early June.<sup>2</sup> During the greater part of this month they exhibit as a rule a normal response to fertilization; and if left unfertilized in sea-water at 20° they undergo the above described coagulative

<sup>1</sup> Instances of this are seen in various phenomena of sensitization. A good instance is the hypersensitiveness to contact induced in frog's skeletal muscle by isotonic solutions of sodium citrate, tartrate, sulphate, and certain other salts. Cf. J. Loeb, *American Journal of Physiology*, 1901, Vol. 5, p. 362.

<sup>2</sup> In former years a considerable proportion of starfish collected in August and September have yielded numerous normal eggs. Probably these starfish were of a different species from the above—presumably *A. vulgaris*. During the last few years this form seems to have become rare in the neighborhood of Woods Hole, and eggs have been difficult to obtain later than June. Two species of *Asterias*, *forbesii* and *vulgaris*, are recognized as occurring in this region; cf. H. L. Clark, Bulletin of the U. S. Fish Commission, 1902, p. 552.

cytolysis within 12 to 15 hours or less. Toward the end of June eggs become fewer and more variable in quality, many fail to mature and the mature eggs on fertilization tend to cleave irregularly and largely die before reaching the blastula stage; a large proportion of eggs show the abnormalities described above; increased resistance to fertilization\* and to cytolytic alteration is especially characteristic and indicates that the plasma membrane has become abnormally resistant to changes in permeability.

I have described the peculiarities of these eggs in sufficient detail above, and have already briefly discussed the physiological nature of the abnormalities. The failure to respond normally to fertilization becomes intelligible on the hypothesis that the essential or critical event in the initiation of cell-division is a temporary and reversible increase in the ionic permeability of the plasma membrane. Such a change involves a decrease in the electrical polarization of the membrane, and it appears probable—as in the analogous case of muscle and nerve—that this change of polarization, and not the mere increase of permeability as such, is the critical event which initiates the rhythmic series of physical and chemical processes of which cleavage is the normal expression.<sup>1</sup> In order that the egg may respond to the contact and entrance of the spermatozoön in a normal manner, its plasma membrane must have a certain definite physico-chemical constitution such that the substances transmitted by the spermatozoön<sup>2</sup> may effect an increase of permeability which in rate and degree approximates a certain norm. This implies a certain degree of resistance to change of permeability; if this resistance is abnormally great, the response fails to occur or is imperfect; if abnormally low, the spermatozoön effects too great and too lasting an increase in permeability

<sup>1</sup> The astral radiations of mitosis are probably the expression of potential differences between different regions of the cell, arising in consequence of altered polarization of the limiting membranes. The alternate appearance and disappearance of the radiations indicates a rhythm of changing polarization of the limiting membranes. For a further discussion cf. my papers in *BIOLOGICAL BULLETIN*, 1909, *loc. cit.*; *Amer. Jour. Physiol.*, 1910, Vol. 26, pp. 128 ff.; *Journal of Morphology*, 1911, Vol. 22, p. 711.

<sup>2</sup> According to Loeb, certain lysin-like bodies (cf. "Entwicklungserregung," p. 247). I have suggested calling these "membranolysins" to indicate the essential nature of their action.

resulting in early death or cytolysis—just as occurs in eggs subjected to a simple membrane-forming treatment without subsequent exposure to hypertonic sea-water.<sup>1</sup> Eggs which begin cleavage, but fragment and break down before proceeding far in development, possibly belong to this latter class. If normal development is to follow fertilization, the properties of the plasma membrane cannot, on the present hypothesis, depart widely from a constant mean or physiological norm.

The failure of the above eggs to respond normally to fertilization, as also their resistance to cytolysis, is thus to be regarded as the expression of a highly resistant condition of the plasma membrane. The latter fails readily to undergo the increase of permeability essential to these changes,—probably because of abnormalities in the nature, state, or proportions of its chemical constituents. The essential effect of the treatment with ether is to restore the normal properties of the membrane. There is, however, no reason to believe that this effect is specific to ether. In some of my last summer's experiments a similar though less favorable effect was produced by exposure to isotonic sodium chloride solution and—in one case—to a 0.1 per cent. solution of chloral hydrate in sea-water. In its general form the problem relates to the essential nature of the modification which these substances induce in the egg, and by which the latter is brought from an irresponsive condition into one in which it shows a normal response. Light is thrown on this problem by the conditions in irritable tissues such as muscle and nerve.

A close analogy exists between the initiation of cell-division in eggs or other resting cells, and the response of an irritable tissue to stimulation. In both cases the initial or critical event is apparently a temporary increase in surface-permeability, with accompanying changes in the electrical polarization of the limiting membranes. The means by which refractory eggs may

<sup>1</sup> The second part of the treatment appears to effect a return of the permeability—which has been increased by the membrane-forming treatment—to the normal (cf. *Amer. Jour. Physiol.*, 1911, Vol. 27, p. 289). Godlewski (*Archiv für Entwicklungsmechanik*, 1911, Vol. 33, p. 225) has independently reached a similar conclusion with regard to the essential nature of the effect produced by the hypertonic sea-water.

be rendered normally responsive is thus analogous to that by which the responsiveness of muscle and nerve to stimulation may be increased. An irresponsive condition in living muscle and nerve may be due to anæsthesia, fatigue, electrotonus, toxic action, or other changes of state. The stimulating action of small doses of alcohol<sup>1</sup> and other narcotics during fatigue suggests an analogy which is probably not without significance. It is known that traces of various lipid-solvent substances very generally increase irritability, or the rate of spontaneous activity, in the most various cells and tissues (leucocytes, cilia, the heart, etc.).<sup>2</sup> The increased responsiveness of the above eggs after ether treatment is a phenomenon of the same general kind. It would appear that the condition of the lipoids in cells determines the readiness of response or the rate of spontaneous activity; and that slight impregnation of the lipoids in the membrane with a lipid-solvent facilitates in this structure the alteration which conditions the permeability-increase and polarization-change of stimulation.

Certain salts markedly increase the irritability of muscle and nerve,—*i. e.*, induce sensitization.<sup>3</sup> Treatment with salt solutions may also restore fatigued muscles to an irritable condition. Frog's skeletal muscles immersed in isotonic sodium chloride solution and made to contract by successive electrical stimuli until irresponsive promptly recover irritability if immersed in isotonic sodium bromide, nitrate or iodide solutions. Sodium iodide restores irritability to muscles which have been fatigued in sodium bromide or nitrate solutions, but chloride has no such action; *i. e.*, the order of the salts cannot be reversed. The restorative effect is rapid, and evidently depends on a surface action, the colloids of the membrane being apparently brought into a condition favorable for stimulation—apparently a condition of increased dispersion.<sup>4</sup> As already described, sodium chloride solution may produce an analogous increase of respon-

<sup>1</sup> The action of small quantities of alcohol in counteracting fatigue in excised frog muscles has been well shown by Lee and Salant, *Amer. Jour. Physiol.*, 1902, Vol. 8, p. 61.

<sup>2</sup> Cf. footnote 2, page 331.

<sup>3</sup> Cf. footnote 1, page 338.

<sup>4</sup> C. Schwarz, *Archiv für die gesammte Physiologie*, 1907, Vol. 117, p. 161.

siveness in refractory starfish eggs. Schwarz's observations, as well as my own with abnormal starfish eggs, thus belong to that general class of cases in which the responsiveness of cells is increased by treatment with salts or low concentrations of lipid-solvents. The response of voluntary muscle to various forms of chemical stimulation may be increased by brief immersion in isotonic solutions of various sodium salts; in the case of salts which do not precipitate calcium, this sensitizing action increases with variation in the nature of the anion in the following general order:  $\text{Cl} < \text{Br} < \text{NO}_3 < \text{ClO}_3 < \text{CNS}$  and  $\text{I}$ , an order corresponding to the order of increasing effectiveness in promoting colloidal dispersion.<sup>1</sup> Interpreted in terms of the membrane theory, these facts mean that the readiness with which the plasma membrane undergoes increase in permeability may be increased either by altering the general state of the colloids in the membrane, or by slightly altering that of the lipoids alone.

We conclude that the effect produced by salts and weak ether solutions in increasing the responsiveness of refractory eggs to fertilization is comparable with the sensitization of irritable tissues by these substances; also that in both cases the essential change consists in an increase in the readiness with which the plasma membrane undergoes the critical change of permeability and of electrical polarization.

It is to be noted that the resistance of eggs to fertilization by foreign sperm may also be decreased by chemical treatment, as Loeb discovered several years ago.<sup>2</sup> Heightening the alkalinity of the medium has this effect. This characteristic and striking effect is probably an expression of a very general action of weak alkali. Many facts indicate that slight increase in the alkalinity of the medium usually increases the readiness with which the permeability of cells is altered: cell-division is accelerated, the irritability of irritable tissues and the rate of activity of automatic tissues is increased, the cytolytic action of salt solutions is accelerated, and in unfertilized eggs membrane formation and the initiation of cleavage may be induced.<sup>3</sup> It remains to be determined whether

<sup>1</sup> R. S. Lillie, *Proceedings of the Society for Experimental Biology and Medicine*, New York, 1910, Vol. 7, p. 170.

<sup>2</sup> J. Loeb, University of California Publications, Physiology, 1903, Vol. 1, p. 1.

<sup>3</sup> Cf. J. Loeb, *Archiv für die gesammte Physiologie*, 1907, Vol. 118, p. 7.

alkali as well as ether can overcome the resistance of over-ripe starfish eggs to fertilization by their own sperm; also whether treatment with weak solutions of ether or other lipoid-modifying substances, as well as with weak alkali, can render cross-fertilization possible. The case of the eggs of hermaphrodite animals, which are irresponsive to sperm from the same individual but not to that of other individuals, may possibly belong in part to the present category. Morgan<sup>1</sup> found that the eggs of *Ciona*, which furnish a typical instance of this behavior, could be fertilized by spermatozoa from the same individual in weak solutions of ether, ammonia or alcohol; but he is inclined to attribute the effect to the stimulating action of these substances on the sperm, rather than to an alteration of the egg. In one experiment, however (p. 147), in which the spermatozoa alone were treated with ether before adding to the egg, few eggs were fertilized, while when both eggs and sperm were so treated the percentage of fertilization was high (in one case 85 per cent. as compared with 4 per cent.). This experiment suggests that the ether produces its effect not merely by increasing the motility of the sperm, but also by altering the condition of the egg, as in the case of *Asterias*. Another interesting case in which the egg is rendered refractory to fertilization has recently been described by Godlewski.<sup>2</sup> If the spermatozoa of *Chaetopterus* and of *Sphærechinus* are mixed, both are found after a few minutes to have completely lost the power of fertilizing the eggs of *Sphærechinus*.<sup>3</sup> Eggs left exposed to this

<sup>1</sup> Morgan, *Journal of Experimental Zoölogy*, 1904, Vol. 1, p. 135.

<sup>2</sup> Godlewski, *Archiv für Entwicklungsmechanik*, 1911, Vol. 33, p. 233.

<sup>3</sup> The spermatozoa in this mixture retain their motility in spite of their having lost the power of affecting the egg (*loc. cit.*, p. 240). It would be interesting to know if the motility undergoes any decrease. Apparently the surface layer of the spermatozoön is modified, since there is no transmission of membranolytic to the egg. This would imply heightened resistance to permeability-change in the plasma membrane of the spermatozoön; and such a change would presumably involve decreased motile activity—i. e., a slower rhythm in the variation of ionic permeability and polarization conditioning the movements. Various facts indicate that in normal fertilization the spermatozoön and the egg affect each other *mutually* in a somewhat similar manner, and that a cytolytic or permeability-increasing action is exercised by the egg upon the sperm as well as by sperm upon the egg. Thus the sperm usually ceases its movements soon after contact with the egg, and often only a portion enters the latter; a cytolytic or disintegrative change in the spermatozoön is thus indicated. The plasma membrane of the sperm might—as apparently in Godlewski's experiments—be rendered sufficiently hyper-resistant to prevent this mutual cytolytic action without entire loss of motility.

sperm mixture are at first unaffected, but in the course of half an hour they become so modified that fertilization with normal *Spharechinus* sperm is impossible. The egg is thus deprived of the power of response to its own spermatozoa.<sup>1</sup> Whether this condition of irresponsiveness (which is comparable to paralysis) may be removed by artificial treatment such as the above has apparently not been determined; but from the analogies with the conditions just described there is every reason to believe that this would readily be found possible.<sup>2</sup>

In conclusion I wish briefly to indicate the bearing of the above observations on the general theory of pathological alterations in cells. The conclusion that many pathological conditions have their primary origin in abnormalities of the limiting membranes of cells is an obvious corollary of any view that regards such membranes—which are essentially insulating surface-films of varying ionic permeability and electrical polarization—as largely controlling the rate and character of the cell-processes. If stimulation depends primarily on altered polarization of the plasma membrane due to increased ionic permeability, it is clear that a normal response, in the case of any cell, implies a definite condition of the membrane. If this condition is permanently altered the cell processes inevitably undergo derangement, and pathological changes follow. Such a deranged condition, if not too far advanced, may be rectified by restoring the membrane to its normal condition. How this may be accomplished is illustrated by the case of the abnormal starfish eggs described above. It is clear from the cytolytic effects produced by many toxins that they cause abnormal increase in the permeability of the membranes; and in all probability their destructive action is in many cases directly due to this surface action. The alteration caused by a toxic agent may consist primarily either in increasing or in decreasing the permeability normal to the membrane, or in altering in either direction the readiness with which the latter undergoes change. Evidently the plasma membrane, as an

<sup>1</sup> A similar and reversible effect may be produced by treating the egg with certain salt solutions, as Mathews and Newman showed some years ago for *Fundulus* eggs; cf. BIOLOGICAL BULLETIN, 1905, Vol. 9, p. 378.

<sup>2</sup> Evidence that this change is in fact reversible is seen in the effects of washing the eggs thoroughly in sea-water after the treatment with the sperm mixture. A partial return of responsiveness to the spermatozoa was observed (p. 236).



insulating—and hence semi-permeable—layer on the integrity of which the normal composition of the living substance depends, cannot undergo marked and prolonged increase of permeability without alteration in the nature and proportion of the cell-constituents; this involves altered chemical organization and eventual derangement of the cell-processes.<sup>1</sup> In most of the abnormal conditions considered above the membrane appears to have undergone the opposite kind of modification, becoming abnormally impermeable and resistant to changes of permeability. Such a condition is essentially one of irresponsiveness, and is in a sense pathological, although it differs from a condition of permanently increased permeability in involving no loss of material from the cell; hence the possibility of restoring the normal properties of the cell—by bringing the permeability again to the normal—should theoretically be greater in this class of cases than in the other.<sup>2</sup>

Perhaps the condition of the above resistant starfish eggs is not properly to be called pathological, since the change in the properties of the eggs toward the close of the breeding season is presumably a constant one, and hence normal in a physiological sense. The eggs merely become hyperresistant to fertilization; *i. e.*, with increasing age the metabolism of the ovaries undergoes alteration so as to lead to the production of eggs having more resistant membranes than before. The cycle of egg-production shortly afterwards comes to a close. The phenomenon bears in certain respects a marked resemblance to senescence, and its conditions may throw light on the physiology of the latter process. In old age the irritable tissues become less and less responsive, and the rate of metabolism is correspondingly lowered. Irre-

<sup>1</sup> I have dwelt on these considerations at somewhat greater length in my earlier paper in this journal, 1909, Vol. 17, p. 197 et seq. The fundamental importance of the part which alterations of the membranes play in pathological processes was first recognized by Zangger. The following quotation will illustrate: "Die normale typische Permeabilität der Membranen ist also Voraussetzung der normalen Lebensfunktionen. Dauernd veränderte Permeabilität der Membranen bedeutet Pathologie, pathologischen Stoffwechsel," etc.: *Vierteljahrsschrift d. Naturf. Ges. Zürich*, 1906, Vol. 51, p. 432. Cf. also *ibid.*, 1907, 1908, and the other papers of Zangger and his students, especially Frei and Stoffel, for a fuller development of these ideas, together with experimental data bearing on the relations of membrane changes to pathological processes, immunity, and related phenomena.

<sup>2</sup> For further discussion of this subject cf. my earlier paper in *American Jour. Physiol.*, 1910, Vol. 26, pp. 112 et seq.

sponsiveness, as already pointed out, implies a state of the plasma membrane in which changes of permeability and of electrical polarization are produced with difficulty. The increasingly resistant character of the membranes implies altered composition. Possibly the condition in over-ripe eggs, as well as in senescence, results from a progressive accumulation or adsorption at the phase-boundaries, *i. e.*, in the membranes, of materials which for some reason are not readily eliminated by the organism.<sup>1</sup> A similar view has recently been expressed by Child.<sup>2</sup> According to his theory "senescence in nature consists physiologically in a decrease in the rate of metabolism, and this is determined morphologically by the accumulation in the cell of structural obstacles to metabolism, *e. g.*, decrease in permeability, increase in density, accumulation of relatively inactive substances, etc." Minot's<sup>3</sup> theory that senescence is the expression of a progressively increasing differentiation of cells, *i. e.*, of an increase in the proportion of separated solid structural material, bears a certain resemblance to this view. The view which I have suggested above is distinctive only in so far as it attributes the essential change to a modification of the *membranes*. It is, theoretically at least, within the possibilities of physiological science to prevent or retard this accumulation of inert materials in the membranes and so to delay senescence. Or the already modified membranes might, if not too profoundly altered, be restored to a normal condition by certain forms of treatment. The simpler the metabolism and the less widely differentiated the tissues, the greater would appear to be the possibility of such "rejuvenescence" of the organism as a whole. In one large group, the Protozoa senescence seems not to be an inevitable occurrence; the earlier interpretation of conjugation as a process whose essential rôle is to counteract an innate tendency to senescence has been discredited by the work of Calkins and Woodruff. The conditions in Metazoa differ from those in Protozoa chiefly in their greater complexity, but probably in no other essential respect.

<sup>1</sup> Probably certain colloidal (*i. e.*, indiffusible) and chemically refractory by-products of metabolism.

<sup>2</sup> Cf. Child, *Archiv für Entwicklungsmechanik*, 1911, Vol. 31, p. 537.

<sup>3</sup> C. S. Minot, "The Problem of Age, Growth and Death." New York and London, 1908.



ANTAGONISM BETWEEN SALTS AND ANÆSTHETICS. —  
I. ON THE CONDITIONS OF THE ANTI-STIMULATING  
ACTION OF ANÆSTHETICS WITH OBSERVATIONS ON  
THEIR PROTECTIVE OR ANTITOXIC ACTION.

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SUBSTANCES which act as anæsthetics, *i. e.*, which render irritable tissues temporarily irresponsive to stimuli or less responsive than normally, or which decrease or abolish reversibly the activity of automatically active tissues like the heart, may belong to the most diverse chemical classes. They may be products of normal tissue metabolism; thus carbon dioxide in certain concentrations acts as a typical anæsthetic; bile salts also depress the irritability of nerve and muscle; the so-called "fatigue substances" may be regarded as belonging to this class; the accumulation of certain undefined metabolic products in the blood of higher animals leads periodically to a condition of normal or physiological narcosis known as sleep. Many inorganic salts also possess anæsthetic property; those of magnesium have the most general action of this kind and the most typical because the most reversible. The depressant action of potassium salts is well known. Calcium and strontium salts in certain concentrations decrease reversibly the susceptibility of muscle and nerve to chemical and other stimulation.<sup>1</sup> In general, electrolytes have marked influ-

<sup>1</sup> After immersion for two to three minutes in isotonic calcium, magnesium, or strontium chloride solution, frogs' voluntary muscle fails to contract, or contracts only slightly, when brought into  $m/8$  KCl or mixtures of  $m/8$  NaCl and  $m/8$  KCl. JOSEPH and MELTZER have also recently demonstrated the anæsthetic action of calcium salts on frogs' muscle and nerve (this Journal, 1911, xxix, p. 1). The action of calcium shows in many irritable tissues a characteristic variation with concentration. BETHE found its omission from artificial sea water to arrest the rhythmical contractions of *Rhizostoma*; addition of a certain proportion

ence on irritability. In some cases acid, in others alkali, show typical anæsthetic action. Bethe found alkali ( $C_{OH} = 10^{-4} N$ ) to check, and acid ( $C_H = 10^{-6}$  to  $10^{-5} N$ ) to accelerate the rhythmical contractions of the *Medusa Rhizostoma*.<sup>2</sup> In the vertebrate heart the reverse is usually observed. Yet traces of acid as well as of alkali heighten the twitching seen in frogs' skeletal muscle in pure isotonic solutions of sodium salts.<sup>3</sup> The effects of a given substance may thus vary from tissue to tissue and from organism to organism, and the same substance in the same concentration may in some cases heighten, in others lower, the irritability of the tissue. Pure solutions of non-electrolytes like sugar show a characteristic anæsthetic action on muscle and nerve.<sup>4</sup> This condition seems general for these tissues, whose irritability normally depends on the presence of sodium salts in their media. It is thus evident that anæsthetic or narcotic action is confined to no class of substances; it is perhaps not too much to say that almost any substance, unless its action is too energetic and hence essentially irreversible (as mercury and silver salts), may in certain concentrations show anæsthetic action, *i. e.*, may temporarily decrease or abolish irritability.

With many substances in certain concentrations the modification of irritability may be in the opposite direction; the tissue becomes temporarily more sensitive to stimuli than normally. Isotonic solutions of sodium citrate greatly increase the irritability of frogs' muscle

was favorable to the maintenance of rhythm; when larger quantities were added the rhythm was again arrested (*Archiv für die gesammte Physiologie*, 1909, cxxiv, p. 561). The action of calcium on the vertebrate heart is similar. Many lipoid-solvent anæsthetics also show a stimulating action in lower concentrations and an anæsthetic action in higher. BETHE, however, found magnesium to show a depressant action from the first; so also aluminium (*Ibid.*, 1909, cxxvii, p. 245).

<sup>2</sup> BETHE: *Archiv für die gesammte Physiologie*, 1909, cxxvii, p. 219.

<sup>3</sup> J. LOEB: *Festschrift für Professor Fick*, Braunschweig, 1899, p. 101. A similar stimulating action of both acid and alkali in low concentrations is seen in the ganglion of the heart of *Limulus*: *cf.* CARLSON: this Journal, 1906, xvi, p. 378.

<sup>4</sup> The anæsthetic action of pure isotonic sugar solutions is shown characteristically in *Arenicola larvæ*; muscular contractions cease within a few minutes in such solutions, while cilia continue; on return to sea water or appropriate salt solutions contractions are resumed. The anæsthetic action of pure sugar solution is similar to that of magnesium chloride solution, though less pronounced. *Cf.* this Journal, 1909, xxiv, p. 463.

and nerve to mechanical and chemical stimuli;<sup>5</sup> pure isotonic solutions of many other neutral sodium salts have a similar though usually less marked effect.<sup>6</sup> Traces of alkali increase the irritability of vertebrate muscle and nerve; increase in the normal ratio of sodium to calcium in the medium has a similar effect on these tissues, while decrease in this ratio lowers irritability.<sup>7</sup> Some substances increase irritability when present in traces, while exhibiting typical anæsthetic action in higher concentrations; this is true of many lipid-solvent anæsthetics; alcohol is a good instance.<sup>8</sup> The influence of certain anæsthetics on growth shows an interesting analogy. It is well known to florists that the presence of a little ether in the air accelerates plant growth; in higher concentrations ether inhibits growth and cell division, as Claude Bernard first showed for seedlings; on removal of the anæsthetic growth is resumed.<sup>9</sup> The same substance may

<sup>5</sup> Cf. J. LOEB: this Journal, 1901, v, p. 362. In general those sodium salts which lower the concentration of the calcium ions in the tissue (in the surface layer? cf. p. 369 of this paper), heighten the contact irritability, both in nerve and muscle.

<sup>6</sup> Pure isotonic solutions of many sodium salts show this action independently of any influence on the calcium compounds of the tissue. The relative activity of the following salts varies with the nature of the anion in the general order: NaCl < NaBr < NaNO<sub>3</sub> < NaClO<sub>3</sub> < NaI and NaCnS — *i. e.*, increases with increase in the promotion of colloidal dispersion. Cf. Proceedings of the Society for Experimental Biology and Medicine, New York, 1910, vii, p. 170.

<sup>7</sup> Cf. J. LOEB: Oppenheimer's Handbuch der Biochemie, 1909, ii, p. 124. This rule, however, by no means holds true for all irritable tissues; removal of calcium from the medium depresses irritability and spontaneous activity in *Medusæ* (BETHE: *Loc. cit.*). Deviation from the optimum proportion of calcium in *either* direction may depress irritability.

<sup>8</sup> The action of traces of anæsthetics (ether, chloroform, chloretone, chloral hydrate) in heightening spontaneous rhythmical activity is well shown in the ganglion of the *Limulus* heart; cf. CARLSON: this Journal, 1906, xvii, p. 182. The same is true for cilia, as ENGELMANN observed. HAMBURGER has recently found that traces of many lipid-soluble substances — iodoform, chloroform, benzol, turpentine, chloral hydrate — increase the phagocytic activity of leucocytes, while stronger solutions decrease this activity; analogous observations were made with spermatozoa. HAMBURGER also points out that a stimulating action in low concentrations is widely characteristic of anæsthetics. Cf. HAMBURGER: Archives Néerlandaises des Sciences Exactes et Naturelles, Série III, B, 1911, i, p. 1. Professor MACFARLANE informs me that traces of ether increase the irritability of *Mimosæ*; higher concentrations produce typical anæsthesia.

<sup>9</sup> C. BERNARD: Leçons sur les phénomènes de la vie communs aux animaux et végétaux, Paris, 1878, chapter vii, pp. 259 *seq.*

thus exhibit diametrically opposite actions at different concentrations. In still higher concentrations most lipoid solvents stimulate irritable tissues strongly, and rapidly cause irreversible or cytolytic alterations, *i. e.*, exhibit a powerful toxic action.<sup>10</sup>

The narcotizing concentration, in the case of any anæsthetic, varies characteristically for different organisms and for different tissues of the same organism. A concentration of ether or chloroform sufficient to abolish completely the normal neuro-muscular or reflex irritability may leave other active tissues almost unaffected; this, of course, is the condition on which the practical use of anæsthetics depends. A good illustration of relative insensitivity to narcotic action in an active tissue is seen in the cilia of many metazoa; these structures, in correspondence with the characteristic automatic and uninterrupted nature of their activity and their irresponsiveness to stimuli, show marked resistance to the action of anæsthetics.<sup>11</sup> Thus the cilia of *Arenicola* larvæ continue their activity for hours in isotonic sugar or magnesium chloride solutions, or in solutions of chloroform or ether which prevent completely all muscular movement. Analogous differences obtain between different organisms. Some are easy, others difficult to anæsthetize. It is noteworthy that a given anæsthetic produces different effects with different organisms; thus chlore-tone is a favorable anæsthetic with cats or rabbits, but not with dogs. Individual differences in susceptibility to narcotic action are also well marked; the effects vary with age, — alcohol and anæsthetics affect children more rapidly than adults, — also with the congenital constitution and to a certain degree with the habits and mode of life of the individual. Different men vary in their susceptibility to the narcotizing action of their own metabolic products, *i. e.*, some resist the onset of sleep more readily than others; such persons seem in general to be relatively resistant to other kinds of narcotic action, as of alcohol. This power of resistance can be increased by use, and it has been observed by surgeons that an acquired resistance to alco-

<sup>10</sup> I have described this action for *Arenicola* larvæ in my paper in this Journal, 1909, xxiv, pp. 30, 31.

<sup>11</sup> Compare OVERTON: Studien über die Narkose, Jena, 1901, p. 185: "Zur Narkose von Pflanzenzellen, Protozoën, Flimmerzellen, etc., sind meistens 6-10-fach höhere Concentrationen der indifferenten Narcotika erforderlich als zur Narkose von Kaulquappen."

hol involves also an increased resistance to anæsthetics. A certain modifiability in the physico-chemical constitution — probably more particularly in the lipid content — of the nerve cells is thus indicated. Wide variation in the quantity and character of the lipid content of different cells is, in fact, a marked characteristic of highly differentiated organisms;<sup>12</sup> and variation in the susceptibility of different organisms and tissues to narcotic action will no doubt be shown, as research advances, to be the physiological correlative of a corresponding variation in lipid content.

At the same time certain broad and significant uniformities are found. The chief of these is the almost universal anæsthetic action of substances, which, however diverse chemically, have in common the physical property of dissolving lipoids or of dissolving in lipoids. The connection between fat-dissolving power and anæsthetic action has long been recognized.<sup>13</sup> Overton and Hans Meyer demonstrated in 1899 a parallelism between the narcotic action of various substances and their oil-water partition coefficient. They refer narcotic action to a modification of the lipoids; permeation of the latter cell constituents with the narcotizing substance is the essential condition of narcosis.

That the lipoids are mainly concerned in certain forms of narcosis may be taken as established. The Overton-Meyer theory, however, in so far as it refers narcosis to modification of the lipoids alone, is inadequate because too special. As we have seen, narcotic action is not confined to lipid solvents; it is merely highly characteristic of them. Why, for instance, do magnesium salts or non-electrolytes exhibit anæsthetic action? The conditions of this similarity of action must be defined in any adequate theory, and in this respect the theory of Overton and Meyer is deficient.

Modification of the lipoids does, however, produce anæsthesia. Why is this? Obviously, in endeavoring to account for a condition so remarkable, we must first consider the probable situation of the lipoids in the cell, since the *locus* of the primary anæsthetic action

<sup>12</sup> Cf. the graphic representation of the relative lipid and protein content of different tissues in W. KOCH's paper, "Recent studies on lipoids," in *Journal of the American Medical Association*, 1911, lvi, p. 799.

<sup>13</sup> First by BIBRA and HARLESS in 1847. For a historical account of the theories of anæsthesia and narcosis, cf. OVERTON: *Loc. cit.*



must correspond to that of the substances whose modification conditions this action. Overton's own work assigns to these substances a special situation; they are to be regarded as concentrated chiefly at the cell periphery, as forming, in fact, an indispensible, perhaps the chief, part of the surface film or plasma membrane. This is shown by the characteristic free permeability of the cell to lipid-soluble substances; such substances, as a rule, gain rapid entrance; others, chemically similar but lipid-insoluble, enter slowly or imperceptibly. Lipid-solvent substances also rapidly modify the osmotic properties of the cell; such substances have a specific action in altering the plasma membrane: even in low concentrations they rapidly destroy the osmotic equilibrium and produce cytolysis. The presence of lipoids in the surface layer must thus be granted; it seems clear also that the state of the lipoids determines the characteristic osmotic properties of this layer. Narcotic action, therefore, if it is identified with lipid-modifying action, must consist primarily in an alteration of the surface film or plasma membrane of the irritable element. How is this effect possible? Why should modification of the plasma membrane alter the irritability of the cell and under certain conditions abolish all power of response?

To answer this question it is necessary to consider the relation of the plasma membrane to the power of response or irritability of the cell. Recent research has shown that this relation is very intimate. In electrical stimulation a change in the electrical polarization of the semi-permeable membranes has been shown by Nernst and his successors, Lucas, Hill, and others, to be the essential or critical event. Theoretically, changes in the polarization of the membrane may result from either of two general causes: (1) changes in the ionic content of the media in contact with the membrane, — this includes, as Nernst showed, the special case of the action of an external current; or (2) modification in the membrane itself, particularly in its ionic permeability or in its power of combining or liberating ions. Normally we find in an irritable tissue a potential difference between the exterior and the interior of the cell or element (equal in muscle to about 0.1 volt), the outer surface being positive; this potential difference appears dependent on the normal impermeable condition of the plasma membrane, since it diminishes or disappears when this structure undergoes marked increase in permeability, as at death or under

the action of cytolytic substances. In other words, the membrane is the seat of a potential difference when impermeable, as normally during rest; this potential difference decreases markedly if the permeability is increased. Now, the potential difference also decreases during stimulation, to return to the normal when stimulation ceases; the effect, in brief, is the same as would be observed if the permeability of the membrane were suddenly and reversibly to increase, and it is difficult to explain it on any other hypothesis. The conclusion we are led to is that the permeability of the plasma membrane undergoes reversible increase during stimulation; stimulating agencies, on this view, are those which increase temporarily, to a sufficient rate and degree, the permeability of the plasma membrane. Direct evidence that an increase of permeability is a normal accompaniment of stimulation is seen in the mode of response of motile plant mechanisms and in various other facts of comparative physiology.<sup>14</sup>

The facts of anæsthesia, interpreted in terms of this theory, indicate that altering the condition of the lipoids in the plasma membrane renders this rapid increase of permeability difficult or impossible under the usual conditions of stimulation. Direct evidence that lipoid solvents prevent an increase in permeability at the same time that they prevent stimulation has hitherto been lacking. Höber has found that in the presence of anæsthetics the action of salts like potassium or rubidium chloride in producing a local negative variation in muscle is checked; and he has interpreted this fact to indicate that stimulation is associated with an alteration of the lipoids, this change being checked or prevented by lipoid solvents.<sup>15</sup> If the local negativity is the expression of local increase in permeability, his observations indicate that anæsthetics render this change difficult, *i. e.*, have an action antagonistic to that of the salt. It can, in fact, readily be shown that anæsthetics may counteract the stimulating action of salts; the twitching shown by voluntary muscle in pure isotonic solutions of sodium salts may be prevented not only by calcium and magnesium salts but also by anæsthetics. I have also found

<sup>14</sup> I have recently attempted to summarize and co-ordinate the main facts and theoretical considerations which indicate that the primary or critical change in stimulation is a rapid and reversible increase in the ionic permeability of the plasma membrane, in this Journal, 1911, xxviii, p. 197.

<sup>15</sup> HÖBER: Archiv für die gesammte Physiologie, 1907, cxx, p. 492. Cf. also Physikalische Chemie der Zelle und der Gewebe, 3d ed., 1911, pp. 488 *seq.*

during the past summer that the permeability-increasing action of isotonic sodium salt solutions is checked by anæsthetics simultaneously with the prevention of the stimulating action. This can readily be shown in the pigmented larvæ of *Arenicola*. As I have already described at length, the stimulating action of pure solutions of sodium and other salts is in this organism associated with the visible permeability-increasing action, seen in the exit of pigment from the cells during the period of strong stimulation. Salts like magnesium or calcium chloride, which check the one effect, also check the other.<sup>16</sup> Marked and rapid increase of permeability appears invariably to involve stimulation. Magnesium salts have an opposite action to sodium or potassium salts; instead of increasing permeability they appear rather to decrease it;<sup>17</sup> at the same time they exert a powerful anæsthetic action. Such facts suggest the view that the essential action of anæsthetics as a class is to *decrease* the normal permeability, thus rendering the increase of permeability requisite for stimulation more difficult. In fact, larvæ transferred from isotonic magnesium chloride solution to  $m/2$  NaCl undergo neither stimulation nor loss of pigment.<sup>18</sup> The same is true for larvæ brought from sea water into appropriate mixtures of sodium and magnesium chloride. The facts to be presented below show a precisely analogous action in the case of the lipoid-solvent anæsthetics. Not only the stimulating and permeability-increasing action, but also the toxic action of pure isotonic sodium chloride solution, is markedly diminished by the presence of the lipoid-solvent anæsthetic in the solution in favorable concentration. There is thus clear evidence, at least in the case of this organism, that the anæsthetic interferes with the stimulating action of neutral salts because of its preventing the rapid increase in permeability which in its absence the salt solution produces; also that the prevention of this effect involves a certain protective or antitoxic action.

#### EXPERIMENTAL.

During the past summer at Woods Hole I have investigated the action of various lipoid-solvent anæsthetics in conjunction with iso-

<sup>16</sup> Cf. this Journal, 1909, xxiv, pp. 23 *seq.*; 1911, xxviii, pp. 210 *seq.*

<sup>17</sup> *Loc. cit.*, p. 25.

<sup>18</sup> This Journal, 1909, xxiv, pp. 480 *seq.*

tonic solutions of neutral salts of sodium and potassium, using the larvæ of *Arenicola* and the unfertilized eggs of starfish and sea urchins.

These experiments have had reference not only to the anti-stimulating action of anæsthetics, but also to their antitoxic action. If pure solutions of, *e. g.*, sodium salts stimulate because of their producing abnormal increase of permeability, and act destructively or as toxic agents for the same reason, — loss of the normal impermeability of the plasma membrane involving abnormal interchanges, with loss of essential protoplasmic constituents as well as of the all-important electrical polarization of the membrane, — any substance which prevents the stimulating action of such solutions should at the same time diminish their toxic action. This is true for calcium and magnesium salts, which when present in small proportions prevent the excessive stimulation and loss of pigment produced in *Arenicola* larvæ by pure solutions of sodium salts, and at the same time exercise a marked antitoxic action. To a certain degree it is also true for anæsthetics, as the experiments described below will illustrate. In the present paper the results of experiments with *Arenicola* larvæ will be described. Those with unfertilized eggs will be described in a separate paper.

The larvæ of *Arenicola* are favorable test objects or physiological indicators for the study of the relations between changes of permeability and stimulation because of the presence within the cells of a yellow pigment which diffuses freely into the medium when the permeability is markedly increased. Rapid increase of permeability sufficient to cause exit of pigment<sup>19</sup> is invariably associated with

<sup>19</sup> This action is cytolytic, and these experiments may be regarded as indicating merely that strong cytolytic action incidentally involves stimulation. The existence of such a constant connection between these two processes is, however, highly significant. What I have maintained is that increase in permeability is the determining condition of stimulation *as well as of cytolytic action*. Conditions which produce marked and rapid increase of permeability may hence have both effects. In general, cytolytic action results when the increase of permeability decidedly exceeds the normal and is essentially irreversible; normal stimulation when the change is temporary, rapid, variable in degree, and completely reversible. Cytolytic substances, in fact, typically produce contraction in frogs' voluntary muscle, but the effect is characteristically irreversible. Naturally, gradations exist between complete and incomplete reversibility of effect; an otherwise normal increase of permeability, if not soon reversed, may lead to irreversible

intense stimulation, as shown by strong and persistent muscular contraction. This effect is produced in a typical manner by pure isotonic sodium chloride solutions. In the experiments described below I have studied the modifications which various anæsthetics produce in this action.

In studying the action of volatile anæsthetics like ether the method used was as follows. The larvæ, which are positively phototactic, are allowed to gather on the light side of a watch glass. Large masses are thus easily collected. Approximately equal quantities are then transferred with pipettes to clean, dry 50 c.c. Erlenmeyer flasks corresponding in number to the several solutions used in the series. After the larvæ have gathered in a mass on the light side of a flask, most of the sea water may be poured off and the remainder largely removed by filter paper without disturbing the larvæ. The solutions to be examined are previously prepared and kept in tightly corked flasks; 20 c.c. of each is added to the larvæ-containing flasks and the latter are instantly corked. The immediate effect of any solution may be readily observed with a strong hand lens or dissecting lens through the bottom of a flask. The larvæ average about 0.3 mm. in length, and there is no difficulty in observing the muscular movements under these conditions; evidence of ciliary movement is seen in the swimming movements; if the ciliary movements are too weak to propel the larvæ and cannot be detected with the hand lens, the low power of the compound microscope may be used, or larvæ may be transferred with a pipette to a watch glass and examined rapidly before the anæsthetic has had time to evaporate. The degree of toxic action of a solution is indicated by the degree of revival of muscular or ciliary movement in larvæ transferred after varying intervals to normal sea water.

The effects of solutions of anæsthetics on *Arenicola* larvæ vary greatly with concentration. Solutions of ethyl ether in sea water in concentrations above 2 vol. per cent (2 c.c. ether plus 98 c.c. sea

changes in the cell; many substances, in fact, produce irreversible or cytolytic effects only when their action is too prolonged. These considerations indicate the general nature of the relationship between stimulating and cytolytic action in the case of any substance; they also indicate why excessive stimulation is injurious to the cell. It is possible that "fatigue substances," like many lipid solvents, are anæsthetic in lower concentrations and cytolytic in higher.

water) produce strong contractions with loss of pigment; the toxic action is also marked. For characteristic reversible anaesthesia the concentration should not exceed 1 vol. per cent; 0.5 vol. per cent checks but does not entirely abolish muscular movement. Similar conditions hold for other anaesthetics; the favorable anaesthetic concentration, which produces complete muscular immobility without loss of pigment or other immediately injurious action, has to be determined empirically for each substance. It is characteristic that in a concentration of anaesthetic sufficient to abolish muscular contraction completely, the cilia continue their activity, sometimes for hours. The various anaesthetics show characteristic differences of action; thus ether is decidedly more injurious to cilia than chloroform, chloretone, or chloral hydrate.

If *Arenicola* larvæ are brought directly from sea water into a series of differently concentrated solutions of ether in .55 m NaCl, strong and persistent muscular contractions accompanied by well-marked loss of pigment are seen in the stronger and weaker solutions as well as in the pure .55 m NaCl. But in solutions of a certain intermediate concentration relatively slight and transient contractions occur and there is little or no immediate loss of pigment. If larvæ are left in such solutions for some hours and are then re-transferred to sea water, contractions are found to return much sooner and more completely than after a similar stay in .55 m NaCl. There has been, in other words, a certain protective or antitoxic action.

Table I gives a summary of a series of such experiments.

The characteristic stimulating and permeability-increasing action of isotonic NaCl solution is thus greatly diminished in the presence of 1 vol. per cent ether. The immediate toxic action is also greatly lessened. Contractions return promptly on transfer to sea water after one and a half hours in the solution; even after twenty-four hours most larvæ show partial revival. The other solutions are less favorable, producing at first marked stimulation and increase of permeability and showing less protective action. Distinct protection is, however, seen in all, if the period of exposure is not too prolonged. Thus, after one and a half hours in Solution 2 there is prompt and well-marked recovery in sea water; but after three and a half hours the larvæ fail to revive, although partial recovery occurs after a similar exposure to the pure solution. This indicates that solutions containing

TABLE I.

| Solution.                             | Immediate effect.                                                                                                                                                                                  | Effect of re-transfer to sea water after exposure to solution for the following periods.                                                                                                                                                                                                                                                  |
|---------------------------------------|----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|-------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| 1.<br>Pure .55 m NaCl.                | { Strong and persistent contraction and marked loss of pigment, relaxation gradual, complete in about one minute. Cilia cease and largely break down.                                              | { Thirty-two minutes. No contractions for about thirty minutes; later they become well marked. No revival of cilia.<br>About two hours. Motionless for about one hour, feeble contractions later in most.<br>Three and a half hours. After two and a half hours only slight and infrequent contractions.<br>Twenty-four hrs. No recovery. |
| 2.<br>.55 m NaCl +<br>2 v. % ether.   | { Strong contraction with marked loss of pigment. Cilia cease and break down.                                                                                                                      | { One hour and twenty-five minutes. Slow contractions in a few seconds, later becoming marked.<br>Three and a half hours. No recovery.                                                                                                                                                                                                    |
| 3.<br>.55 m NaCl +<br>1.5 v. % ether. | { Strong contraction, but relatively rapid relaxation. Moderate exit of pigment, decidedly less than in Solutions 1 and 2. Cilia checked at first, but become active later; cease within one hour. | { One hour and twenty-three minutes. Contractions return at once, later all show active contractions.<br>Three and a half hours. Well-marked contractions return after a considerable delay.<br>Twenty-three and a half hours. No recovery.                                                                                               |
| 4.<br>.55 m NaCl +<br>1 v. % ether.   | { Larvæ contract on contact of solution, but relax at once. Almost no exit of pigment. Cilia cease at first, but revive in two to three minutes; cease again within one hour.                      | { One hour and twenty-five min. Active contractions at once.<br>Three and a half hours. Contractions return after a delay of about twenty minutes, later they become vigorous and frequent.                                                                                                                                               |
| 5.<br>.55 m NaCl +<br>0.7 v. % ether. | { Well-marked contraction, but relaxation prompter and loss of pigment less than in the pure solution.                                                                                             | { Twenty-three hours. Contractions return gradually in a large portion.<br>Three hours and twenty-five minutes. Contractions return gradually, next day all show well-marked movements.                                                                                                                                                   |
| 6.<br>.55 m NaCl +<br>0.5 v. % ether. | { Shows no distinct difference from the pure solution.                                                                                                                                             | { Four hours and twenty min. Recovery is slight, but greater than after similar exposure to the pure solution.                                                                                                                                                                                                                            |

this proportion of ether are at first less destructive to the tissues than the pure solution, though later they become more so. It is noticeable that after twenty-four hours in Solution 2 swelling and general

disorganization are more advanced than in the pure solution; while in Solution 4 (with 1 vol. per cent ether) these changes are distinctly lessened. The cytolytic action of the pure solution is thus checked by ether in the lower concentration, while in the higher the cytolytic action of the ether is added to that of the salt and disintegration is accelerated.

In the above experiments the larvæ were transferred directly from normal sea water to the ether-containing salt solution. If they are first anæsthetized in sea water and then brought into the salt solution, the stimulating and permeability-increasing effects are prevented much more completely, even with only 0.7 vol. per cent or 0.5 vol. per cent ether, and the protective action is still more striking.

The following experiments will illustrate:

June 20, 1911, 10.05 A. M. Arenicola larvæ are brought into a solution of .7 vol. per cent ether in sea water. Muscular contractions cease at once, cilia continue. There is no trace of pigment extraction. After seven minutes (10.12) larvæ are brought from the above solution into .55 m NaCl containing .7 vol. per cent ether. There is no visible effect at first, — neither contraction nor loss of pigment. The larvæ remain elongated and rigid and continue slowly swimming by their cilia. In five hours the cilia have largely ceased; the larvæ are then extended and motionless; there is no trace of pigment in the solution.

After five hours in the solution (at 3.14) the larvæ are transferred to sea water. Slight muscular contractions reappear in a few seconds, the cilia also revive. In one hour all show well-marked muscular and ciliary movements. Next day, eighteen hours later, all show active muscular movements; the cilia are also active in most.

*Control.* — Larvæ transferred immediately from sea water to .55 m NaCl (about 10.00 A. M.) show instant prolonged contraction with loss of pigment. The cilia cease movement and largely disintegrate within a few minutes.

Transfer to sea water after five hours in the pure solution (3.24) produces no immediate effect. Two hours later (5.44) slight muscular contractions are seen at intervals in a few larvæ, but no ciliary movement. Next day almost all are motionless and apparently dead; faint movements are seen in one or two.

It is evident, on comparing the above two series of experiments, that when transfer is made directly from sea water to the ether-containing salt solution, the salt may produce well-marked increase



of permeability and stimulation before the anæsthetic action of the ether has had time completely to assert itself; these effects are, however, checked and rapidly reversed, as seen in the prompt relaxation and the relatively slight loss of pigment, and also in the protective action. If the organisms are previously anæsthetized in sea water, the ether-containing salt solution has no evident action at first and only gradually asserts its toxic action. It is noteworthy that under these conditions the cilia remain active for some hours in the ether-containing salt solution, whereas, without previous anæsthetization they cease movement comparatively soon, though more gradually than in the pure salt solution. When it is considered that pure isotonic sodium chloride solutions rapidly disintegrate these structures, the efficacy of the protective action of the anæsthetic will at once be apparent.

Larvæ were also transferred from sea water containing 0.7 vol. per cent ether to pure 0.55 m NaCl. A moderate contraction results at first with slight loss of pigment. After five minutes considerable pigment is extracted on shaking; after twenty minutes the solution contains almost as much pigment as the control (in which larvæ were brought directly from normal sea water into 55 m NaCl). The injury to cilia and muscle is, however, more gradual than in the control; slight muscular contractions persist after one and a half hours in the solution and a few cilia remain active. The immediate toxic action of the pure salt solution is thus somewhat lessened if the larvæ are brought into it while in a state of anæsthesia. Rapid action thus seems an essential condition of the marked injury produced by direct transfer to the salt solution. In the presence of the anæsthetic the action is retarded and the injury is less far-reaching. This experiment is analogous to the one cited above in which larvæ were brought from isotonic magnesium chloride into sodium chloride solution. In this case, however, the stimulating and destructive effects are prevented to a much greater degree than in the experiment with ether just described.

Solutions of other anæsthetics in sodium chloride solution produce effects essentially similar to the above, although their precise nature varies from substance to substance, each showing characteristic specific peculiarities of action. The main results of my last summer's experiments may be briefly summarized as follows:

*Chloroform.* — In concentrations of one eighth to one tenth saturated in sea water, chloroform anæsthetizes the musculature rapidly and completely without any extraction of pigment. The cilia remain active in such solutions and the larvæ gather in groups or clumps. One sixth saturated solutions cause at first some loss of pigment, but otherwise show similar action. Prompt recovery of contractions follows return to sea water even after many hours in such solutions. In higher concentrations chloroform produces well-marked loss of pigment and contraction, the cytolytic and toxic effects becoming more pronounced as the concentration increases. Saturated solutions are almost instantly fatal.

Larvæ transferred directly from normal sea water to .55 m NaCl one sixth saturated with chloroform contract strongly at first, but almost instantly relax; there is a slight loss of pigment, but much less than in the pure solution; ciliary movement continues, and the larvæ swim actively for some time; no muscular contraction is seen during the stay in the solution. Chloroform has decidedly greater protective action on cilia than ether. Even after eighteen hours in the above solution slow ciliary movement persists in many larvæ. The protective or antitoxic action on the muscle cells is also very decided; transfer to sea water after eighteen hours in the solution is followed within a few minutes by a well-marked revival of muscular contractions; later active contractions are renewed in all larvæ. Similar exposure to the pure .55 m NaCl is completely fatal to the vast majority of larvæ.

*Ethyl alcohol.* — Larvæ brought from sea water into .55 m NaCl containing 5 vol. per cent alcohol show only slight temporary contraction followed by rapid relaxation; there is no appreciable loss of pigment; even after five hours the solution remains colorless. Muscular contraction ceases instantly, ciliary movement within ten minutes. On return to sea water after one and three fourths hours the cilia revive at once; muscular contractions are resumed after a delay of about ten minutes. After three and a half hours in the solution there is partial revival of cilia on return to the sea water; muscular contractions reappear gradually but completely. After five and a half hours the cilia are destroyed; active muscular contractions return in sea water, though gradually. After twenty-two hours in this solution the pigment is largely extracted, and there is no recovery

in sea water. Alcohol thus shows decided antitoxic action at first, in correspondence with its marked effectiveness in checking increase of permeability and stimulation; later it shows itself less effectual than ether or chloroform in protecting against the more prolonged action of the salt solution. After a day in the alcohol-containing solution the larvæ are all dead and partly depigmented.

*Chloretone.* — Solutions of this substance in .55 m NaCl also prevent the immediate stimulating and permeability-increasing action. Chloretone shows the most striking action of any anæsthetic so far studied. The following experiments will illustrate. Larvæ were transferred directly from sea water to the following solutions. The effects observed were as follows:

1. *Saturated solution of chloretone in .55 m NaCl.* — There is no immediate contraction or loss of pigment, but in half a minute the larvæ shorten to two thirds length, and loss of pigment begins; in three minutes the solution is tinged slightly yellow; within an hour it is deeply colored, and the larvæ show marked disintegration.

2. *.55 m NaCl half saturated with chloretone.* — No contraction and no loss of pigment; the solution remains perfectly colorless for several minutes; the cilia remain slowly active. In ten minutes the solution is faintly yellow; by forty minutes it has the same color as the control; the larvæ are now motionless and begin to show signs of disintegration. Return to sea water after an hour in this solution has no reviving effect.

3. *.55 m NaCl one fourth saturated with chloretone.* — No contraction or loss of pigment; after an hour the solution is still colorless; the larvæ are then rigid, but otherwise normal-looking; the cilia are slowly active. In two and a half hours some pigment is extracted; the cilia have ceased by then. Transfer to sea water after forty-nine minutes is followed by complete revival of muscular contractions. Similar transfer after two and a half hours produces only imperfect and partial recovery; next day the majority of larvæ are found dead and disintegrated.

4. *.55 m NaCl one sixth saturated with chloretone.* — No contraction or loss of pigment. After two hours the solution is still colorless; the larvæ are rigid, with slowly active cilia. Larvæ returned to sea water after two hours show perfect recovery of muscular contractions. After seventeen hours in the solution many revive in sea water, though imperfectly.

The above experiments show that with the four anæsthetics, ether, chloroform, alcohol, and chloretone, the onset of the anæsthetic action is so rapid as to prevent or greatly check the stimulating and perme-

ability-increasing action of isotonic sodium chloride solutions, even when the organisms are suddenly transferred directly from sea water to the anæsthetic-containing salt solution.

Other anæsthetics have a more gradual action and are unable to prevent the initial stimulation and increase of permeability, although they may afterward show distinct protective or antitoxic action. Chloral hydrate, ethyl urethane, benzol, toluol, and xylol belong to this class.

*Chloral hydrate.*—In isotonic NaCl solutions containing chloral hydrate in the concentrations 0.8, 0.5, 0.3, 0.2, and 0.1 per cent the characteristic persistent strong contraction and loss of pigment occur essentially as in the pure solution. In the 0.3 per cent and 0.2 per cent solutions considerable protective action is seen both for muscle and cilia; recovery in sea water after four or five hours in these solutions is decidedly more complete than after the same exposure to the pure solution.

*Ethyl urethane.*—Similarly with urethane in the concentrations 0.6, 0.5, 0.4, and 0.2 per cent. The typical contraction, loss of pigment, and destruction of cilia result when larvæ are brought directly from sea water into these solutions. Some protective action was observed in 0.4 per cent and 0.2 per cent urethane solutions, but not in the others.

*Benzol, xylol, toluol.*—Solutions of these aromatic hydrocarbons in 0.55 m NaCl, in saturated, two thirds saturated, and half saturated concentrations, also produce in all cases marked contraction and loss of pigment. The recovery of muscular contractions in sea water after two and a half hours in the two thirds and half saturated solutions is more complete than after a similar stay in the pure salt solution. Even after five hours in the two thirds saturated solutions distinct protective action is seen. The destruction of cilia by the salt solution is also checked. The saturated solutions show a certain protective action during the first hour, but later prove more toxic than the pure salt solution. The differences between the three hydrocarbons are inessential.

Experiments on the action of anæsthetics in conjunction with solutions of other sodium salts have not yet been tried. Pure isotonic solutions of such salts have an action on *Arenicola* larvæ similar to that of the chloride, and their stimulating and permeability-increasing

action is similarly checked by calcium, though to a degree varying with the nature of the salt.<sup>20</sup> It is thus to be expected that in their relation to anæsthetics they will also be found similar to the chloride.

*Anæsthetics and potassium salts.* — Isotonic KCl solutions produce in *Arenicola* larvæ an intense persistent muscular contraction accompanied by marked loss of pigment; the latter effect is distinctly more pronounced than with NaCl. If equal quantities of larvæ are brought from sea water into equal volumes of the two solutions, the .55 m KCl is invariably found, after the first minute, to be decidedly more deeply tinged with pigment than the .55 m NaCl. In correspondence with this difference it is found that the stimulating action of KCl is decidedly the stronger of the two; this is proved by the fact that the above anæsthetics are unable to counteract it to more than a slight degree. The following experiments will illustrate:

July 2, 1911. Larvæ were transferred as above from sea water to the following solutions: (1) 0.55 m KCl, (2) 0.55 m KCl + 1 vol. per cent ether, (3) 0.55 m KCl +  $\frac{1}{2}$  saturated chloroform, (4) 0.55 m KCl + 5 vol. per cent ethyl alcohol. In all four solutions there occurred at once the characteristic intense muscular contraction with simultaneous loss of pigment; the only evident effect of the anæsthetic was a somewhat less gradual relaxation in Solutions 2 and 3; the immediate loss of pigment was also somewhat decreased in Solution 2.

Though the immediate action of KCl is more intense than that of NaCl and hence shows little or no counteraction by the anæsthetic, a certain protective action is nevertheless shown later; larvæ transferred from Solutions 2 and 3 to sea water after intervals of respectively two and a half, six and a half, and twenty hours showed more complete recovery than after the same exposures to the pure solution. After twenty hours in pure .55 m KCl the larvæ are swollen and partly disintegrated, and there is no revival of contractions in sea water; in solutions containing ether and chloroform as above the swelling and disintegration are distinctly less than in the pure solution, and a certain proportion of larvæ recover contractility in sea water. Alcohol, on the other hand, showed no definite antitoxic action.

As with sodium chloride, the immediate effects of the anæsthetic-containing .55 m KCl are less pronounced if the larvæ are anæs-

<sup>20</sup> Cf. this Journal, 1911, xxviii, p. 212.

thetized in sea water previously to being brought into the solutions. Larvæ transferred from sea water containing 0.6 vol. per cent ether to pure .55 m KCl contract and lose pigment, but there is a distinct delay in both effects; if similarly transferred to KCl solutions containing ether, chloroform, or alcohol, as above, the delay is much greater; there is a relatively gradual contraction beginning after a few seconds, and pigment diffuses slowly into the solution; the latter is well tinged with yellow after a few minutes, but less so than the pure solution; later this difference disappears, and the protective action is found to be no greater than in larvæ brought directly from normal sea water into the same solutions.

Thus the presence of the anæsthetic in KCl solutions, while retarding the stimulating and permeability-increasing action, is not able entirely to prevent these effects, as in the case of NaCl solutions. Evidently the action of the KCl in increasing permeability is more energetic and hence more difficult to counteract than that of NaCl.<sup>21</sup>

*Anæsthetic action of magnesium salts.* — I have already described this action in several previous papers cited above. Larvæ transferred from sea water to pure isotonic solutions of magnesium salts exhibit neither contraction nor loss of pigment; all muscular movement ceases in a few seconds, though the cilia continue their activity. If larvæ are then transferred from such solutions to pure .55 m NaCl, little or no contraction results and there is no loss of pigment. Such larvæ are also less rapidly injured by the pure NaCl solution; *i. e.*, the previous treatment with magnesium chloride has well-marked protective effect. Transfer of normal larvæ from sea water to appropriate mixtures of sodium and magnesium chlorides, or sodium and calcium chlorides, produces only slight stimulation unaccompanied by loss of pigment, and in such solutions the typical antitoxic action is seen. These effects are directly analogous to those seen with lipid solvents.

<sup>21</sup> Rather singularly, although the immediate stimulating and permeability-increasing action of isotonic KCl solution is more pronounced than that of NaCl (a fact agreeing with the conditions in vertebrate muscle), prolonged exposure (some hours) to  $m/2$  KCl is less injurious than to  $m/2$  NaCl (*cf.* my paper in this Journal, 1909, xxiv, p. 459, Tables IX and X, pp. 488, 490). Possibly the immediate strong action of the KCl is succeeded by a secondary permeability-decreasing action which retards further breakdown for a time. In lower concentrations potassium depresses irritability without toxic action.

The rapid increase of permeability with the associated stimulating and toxic action is checked or prevented by the magnesium or calcium or other antitoxic salt.

#### CONCLUSION.

The foregoing experiments indicate clearly the fundamental importance of the limiting layer or plasma membrane in anæsthesia. So far as my observations with *Arenicola* larvæ have extended, the intensity of the stimulating action produced by salt solutions shows a definite parallelism with the degree of permeability-increasing action as indicated by the liberation of pigment from the cells. Substances, whether salts or "anæsthetics," which check or prevent the permeability-increasing action of the pure salt solution also check or prevent stimulation by this solution.<sup>22</sup> These experiments also indicate clearly that the toxic action exerted by the pure salt solution is due in large part to the destruction of the normal semi-permeable properties of the plasma membrane, since prevention of the initial rapid increase of permeability has, together with the anti-stimulating, a marked protective or antitoxic action. There is thus experimental evidence that anæsthetics produce their characteristic effects not by entrance into the cell, but by a characteristic surface action, consisting in an alteration of the normal properties of the limiting surface film or plasma membrane of the cell.<sup>23</sup>

The nature of the general theory of anæsthesia to which the foregoing facts and considerations directly point will be already evident. Anæsthetics are substances which render the plasma membrane of the irritable tissue more resistant than normally to changes of permeability. They may at the same time render the membrane even less permeable than in the normal resting state; magnesium chloride

<sup>22</sup> It should, of course, be noted that such substances also prevent *normal* stimulation, as shown by their characteristic anæsthetic action in sea water.

<sup>23</sup> Lipoid solvents enter the cell immediately, as OVERTON has shown, and a portion of the anæsthetic action might conceivably be attributed to this entrance. But magnesium salts, which have equally characteristic anæsthetic action, enter the cell very slowly, if at all. Yet anæsthesia is complete after a few seconds in  $m/2$   $MgCl_2$  solution. The same is true of isotonic sugar solution, though in this case the action is slower. The essential change in anæsthesia must be *superficial*, in these cases at least.

appears thus to affect the cells of *Arenicola* larvæ; but the essential effect is to deprive the irritable elements of their characteristic property of responding to changes of condition by rapid and reversible changes of permeability. This property seems to be the essential peculiarity of irritable tissues. Any substance or condition, such as anelectrotonus, which so alters the membrane as to deprive it temporarily of this property has anæsthetic action.

A complete theory of anæsthesia implies a complete theory of stimulation, and this has not yet been attained. It is agreed, however, that the most constant feature of the latter process is its association with a temporary decrease in the potential difference between the outer surface and the exposed interior of the irritable element. The same effect follows any marked increase in surface permeability, however induced; rapid increase of permeability also produces strong contractions in muscle, as already seen. On the membrane theory the electrical variation of stimulation is simply the expression of a depolarization of the limiting membrane of the irritable element, consequent on temporary increase in ionic permeability. Any sufficient increase in permeability due to cytolytic or other action results in a similar depolarization and hence under certain conditions in stimulation. Rapid depolarization of the plasma membrane thus appears to be the critical or primary event in stimulation. Nernst has shown that electrical stimulation involves a sudden change in the electrical polarization of the semi-permeable boundary surfaces of the irritable tissue; the existence of a demarcation current in the resting tissue during life indicates that these surfaces are normally the seat of an electrical polarization; and the law of polar stimulation indicates that the external electrical current stimulates where its effect is suddenly to diminish this pre-existent polarization. The conclusion follows — if we grant that stimulation involves an increase of surface permeability — that the degree of electrical polarization of the membrane *determines* its permeability, depolarization corresponding to or inducing increased permeability. A similar interdependence between the electrical condition of the membrane and its permeability has been observed by Girard for membranes of pigs' bladder and other materials. The facts of electrical stimulation thus lead directly to the assumption of a reciprocal interdependence between the degree of permeability of the plasma membrane and the



degree of its electrical polarization, — variation in the one condition-  
ing a corresponding variation in the other. This seems to be the  
essential condition on which irritability, or the possibility of electrical  
or other stimulation, depends.

We are thus led to conceive of the plasma membrane in irritable  
tissues as a structure having the following essential properties: a  
thin colloidal surface film, partly lipoid, partly protein, containing  
electrolytes and other substances (partly in a state of adsorption),  
highly impermeable (during rest) to dissolved substances of low  
molecular weight (unless lipoid-soluble); and the seat of an electrical  
polarization of such a kind that the outer surface has during rest a  
potential about 0.1 volt higher than the inner. This potential differ-  
ence is itself an essential factor in determining the permeability of  
the membrane, — its decrease, even to a slight degree, resulting in an  
increase in permeability which in highly irritable tissue may be very  
pronounced and rapid.<sup>24</sup> Such a condition of increased permeability  
and depolarization will necessarily spread — because of the electrical  
effects in its immediate neighborhood — from the point of stimula-  
tion over the whole membrane.<sup>25</sup>

In anæsthesia it is to be assumed that the membrane is so altered  
that it fails to respond to a change in its electrical polarization by  
an increase in its permeability. This failure, as we have seen, may be  
due to a general action on the colloids of the membrane or to an action  
confined at first to the lipoids. Why alteration of the colloids should  
thus alter the properties of the membrane cannot be said at present  
with any definiteness; it is known, however, that the permeability  
of colloidal membranes depends on the condition of the colloids, and  
that this permeability can be altered by electrolytes.<sup>26</sup> Ready reversi-

<sup>24</sup> The conception of a membrane whose permeability may change reversibly  
within a period of .001 second or less — as the facts of nerve stimulation indicate  
— may seem inadmissible to many; yet the difficulty is of the same nature as —  
and certainly no greater than — the difficulty of accounting for the rapidity of  
alternate contraction and relaxation in the colloidal fibrils of muscle cells and  
cilia. If the state of tension of a colloidal fibril can vary so rapidly as we observe  
to be the case, there is no reason to doubt that the state of ionic permeability  
of a colloidal membrane can vary with at least equal rapidity.

<sup>25</sup> For a fuller discussion of this point *cf.* my paper in this Journal, 1911, xxviii,  
pp. 217 *seq.*

<sup>26</sup> *Cf.* ZANGGER'S review in *Ergebnisse der Physiologie*, 1908, vii, pp. 143 *seq.*

bility of colloidal aggregation state is presumably a necessary condition of irritability, and the depressant or anæsthetic action of salts of alkali earth or heavy metals may be due to their decreasing the readiness or the reversibility of aggregation changes.<sup>27</sup> It is also far from clear why changing the state of the lipoids should so alter the properties of the membrane. Investigators are not agreed as to the nature of the relations between the lipoids and the other colloids of the cell, — *i. e.*, whether there is combination, simple intermixture, or some definite structural arrangement, mosaic-like or otherwise. The suggestion that the lipoids have a "protective" influence on the other colloids of the membrane — limiting their changes of aggregation state — renders certain facts somewhat more intelligible; *e. g.*, why in the presence of chloroform and ether the isotonic NaCl solution has relatively little immediate action on the membrane and fails to break down the cilia. NaCl and other electrolytes unquestionably increase the permeability of the membrane by altering the state of colloidal dispersion;<sup>28</sup> and this effect is in fact checked or prevented if the tissue is previously impregnated with the anæsthetic.

With reference to the precise manner in which the state of the lipoids is modified during anæsthesia by lipoid solvents, there are several possibilities to be considered. Any purely solvent action is precluded, since the effect is characteristically reversible; this consideration has been dwelt on by Overton in his book on narcosis.<sup>29</sup> A second possibility is that the state of colloidal dispersion of the lipoid is altered — presumably increased; this, however, seems to be inconsistent with the observation of Koch that there is no relation between the anæsthetic properties of a lipoid solvent and its ability to hinder the precipitation of lecithin by calcium.<sup>30</sup> The third possibility, and the one which seems best fitted to account for the phe-

<sup>27</sup> The reversibility of the aggregation changes produced by salts in solutions of proteins shows a general decrease in the order alkali, alkali earth, and heavy metal salts. Cf. PAULI: Beiträge zur chemischen Physiologie und Pathologie, 1905, vi, p. 233.

<sup>28</sup> The action of the pure isotonic NaCl solution on the membranes is probably essentially similar to its action on the cilia which are visibly broken down or transformed into droplets or granules after a few minutes in the solution.

<sup>29</sup> Page 51.

<sup>30</sup> Cf. W. KOCH: Journal of pharmacology and experimental therapeutics, 1910, ii, p. 249.

nomena observed, is that there is no change in the state of dispersion of the lipid, — *i. e.*, in the *number* of colloidal particles, — but simply an alteration in the relative dimensions of the lipid and other colloidal particles in the membrane, — *i. e.*, in the volume occupied by these several constituents. The anæsthetic tends to become distributed between the lipid particles and the other solvents present in accordance with its characteristic partition coefficients between these solvents and water; the accumulation of the lipid solvent in the colloidal particles of lipid is thus favored; hence the latter undergo increase in size or swell. The colloidal particles in a lecithin suspension do, in fact, undergo an evident increase in size in the presence of ether or chloroform.<sup>21</sup> This change is reversible, like all changes involving simple solution, and may occur independently of any change in the state of dispersion, — *i. e.*, in the number of particles. Its effect on the membrane will be to alter the structural consistency of the latter in a definite and perfectly reversible manner. It is to be inferred that after the lipid particles have increased in volume beyond a certain degree the membrane becomes incapable of responding to the stimulating agency by a rapid increase in its permeability as normally. It remains instead permanently impermeable, a condition corresponding to inexcitability.

Certain current hypotheses attribute anæsthetic action to a direct suppression of processes which are rather to be regarded as secondary consequences of stimulation than as inherent in the nature of the stimulation process itself. Thus the view that anæsthetics produce their effects by retarding or preventing intracellular oxidations has been adopted by several investigators, notably by Verworn.<sup>22</sup> The main difficulty with this view is that anæsthesia is as characteristic of nerve, where oxidations are slow and not evidently increased during stimulation, as of muscle, where they are enormously accelerated. Moreover, cyanides, which characteristically suppress oxidations, only gradually lower the irritability of nerve.<sup>23</sup> Again Warburg has shown that sea urchin eggs may be anæsthetized — so as to arrest cleavage

<sup>21</sup> Cf. CALUGAREANU: *Biochemische Zeitschrift*, 1910, **xxix**, p. 96.

<sup>22</sup> Cf. VERWORN: "Ueber Narkose," *Deutsche medizinische Wochenschrift*, 1909, No. 37.

<sup>23</sup> Cf. DONTAS: *Archiv für experimentelle Pathologie und Pharmacologie*, 1908, **lix**, p. 430.

— without notably altering the rate of oxidations.<sup>34</sup> On the present view the increase in oxidations in such a tissue as muscle is to be regarded as one of the secondary effects of stimulation; prevention of stimulation necessarily involves a suppression of oxidations in this tissue, but only because an increase in oxidations is here an essential consequence of stimulation. Naturally, all of the effects that normally follow stimulation, including the increase of oxidations, are checked or prevented during anæsthesia. The facts already adduced indicate clearly that the primary anæsthetic action consists in an alteration of the limiting membrane of the irritable tissue. From the general facts of electrical stimulation we must conclude that in muscle rapid changes in the electrical polarization of the membrane involve in some manner a marked acceleration of oxidations; the precise conditions of this effect are insufficiently understood. It is, however, to be regarded as highly significant that during the height of stimulation in voluntary muscle there is a rapid rhythmical fluctuation of the action current,<sup>35</sup> indicating on the present theory a corresponding rhythmical variation in the electrical polarization of the plasma membrane; this would involve similar changes in the electrical polarization of the other electrically polarized surfaces within the system enclosed by such a membrane, and it appears highly probable that the high rate of oxidation in active muscle is to be referred to this condition.<sup>36</sup> Anæsthetics, by rendering impossible such rapid changes of polarization in the membrane, would prevent the increase in oxidations normally following stimulation. On such an hypothesis the manner in which alteration of the plasma membrane may modify the oxidations within the cell, and prevent their increase by stimulating agencies, becomes at least partially intelligible.

<sup>34</sup> WARBURG: *Zeitschrift für physiologische Chemie*, 1911, lxx, p. 413.

<sup>35</sup> Cf. the papers of GARTEN, PIPER, DITTLER, and F. BUCHANAN; for references cf. FRÖHLICH: *Sammelreferat: über die rhythmische Natur der Lebensvorgänge*, *Zeitschrift für allgemeine Physiologie*, 1911, xiii.

<sup>36</sup> I find that the oxidative formation of indophenol in frogs' blood corpuscles — which, it should be noted, shows a characteristic relation to the nuclear surface (cf. my paper in this Journal, 1901, vii, p. 420) — is markedly accelerated, especially in leucocytes, by passing induction shocks through a thin layer of suspended corpuscles on a slide. Rapid alternation of polarization and depolarization at the active surfaces evidently furthers this particular oxidation at least. These experiments will be described in a later paper.

## SUMMARY.

The chief experimental results and conclusions of the present paper may be briefly summarized as follows:

1. In the presence of ether, chloroform, alcohol, and chloretone, in concentrations corresponding to those which produce typical anæsthesia, pure isotonic solutions of sodium chloride no longer produce in *Arenicola* larvæ the typical strong muscular contractions, accompanied by marked loss of pigment, which characterize the action of the pure solution. The anæsthetic thus prevents rapid increase of permeability at the same time that it prevents stimulation.

2. The presence of anæsthetics also markedly retards the injurious action of pure solutions of sodium chloride on the muscles and cilia of these organisms. Anæsthetics thus show, in concentrations that produce anæsthesia, a well-marked protective or antitoxic influence similar to that of calcium or magnesium chloride. This influence is also to be referred to a prevention of the cytolytic or permeability-increasing action of the pure salt solution on the plasma membranes.

3. Other anæsthetics — chloral hydrate, urethane, benzol, xylol, toluol — are more gradual in their action; they show a more or less distinct protective or antitoxic influence, but do not prevent the immediate stimulating and permeability-increasing action of isotonic NaCl solutions. On the other hand, isotonic magnesium chloride solutions rapidly anæsthetize the larvæ, and completely prevent stimulation and increase of permeability on subsequent transfer to .55 m NaCl; the protective or antitoxic action is also pronounced.

4. The general conclusion is drawn that anæsthetic action consists essentially in an alteration of the surface film or plasma membrane of the irritable element, of such a kind that the rapid and reversible increase in ionic permeability, which is the primary or critical change in stimulation, is rendered difficult or impossible. The cell is at the same time rendered more resistant to those forms of toxic action which consist in an abnormal increase of surface permeability.





ANTAGONISM BETWEEN SALTS AND ANÆSTHETICS.—II.  
DECREASE BY ANÆSTHETICS IN THE RATE OF TOXIC  
ACTION OF PURE ISOTONIC SALT SOLUTIONS ON  
UNFERTILIZED STARFISH AND SEA-URCHIN EGGS.

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INTRODUCTORY.

IN a recent paper<sup>1</sup> I have shown that various anæsthetics (ether, chloroform, alcohol, chloretone, chloral hydrate, benzol, toluol, xylol), in concentrations identical with those which produce typical anæsthesia, prevent or retard the disintegrative or toxic action of pure isotonic solutions of sodium chloride on the cilia and muscles of *Arenicola* larvæ. This antitoxic action is associated with a decrease or prevention of the marked and rapid increase in permeability which the pure salt solution acting by itself normally produces. The protective or anticytolytic action of the anæsthetic is thus to be referred to its action on the plasma membrane, — this structure being so modified that the salt solution is no longer able to induce the same marked and rapid increase of permeability as before. Anæsthetics thus produce an effect similar — though less favorable — to that of salts like calcium or magnesium chloride, which also prevent rapid increase of permeability and at the same time diminish the toxicity of the pure salt solution. Further proof is thus afforded that certain forms of

<sup>1</sup> This Journal, 1912, xxix, p. 372.



antitoxic action depend primarily on a modification of the impermeable surface layer or plasma membrane of cells, and consist in rendering this structure more resistant to conditions that in the absence of the antitoxic agent increase permeability to an abnormal and injurious degree.<sup>2</sup>

In the present paper I shall describe the results of similar experiments with the unfertilized eggs of starfish and sea-urchins. In each series of these experiments the eggs were exposed for definite periods to (1) the pure isotonic solution of the salt used, and (2) to a series of solutions containing in addition to the salt various anæsthetics in known concentrations. In the majority of series calcium chloride and potassium cyanide were also used for comparison. The relative toxicity of the solutions was estimated (1) by observing the rate of cytolytic action upon the eggs while in the solution; this action is shown in *Asterias* eggs by a gradual darkening or coagulation of the protoplasm, and in *Arbacia* eggs by the diffusion of pigment into the solution; and (2) by fertilizing the eggs in sea water after a definite stay in the solution and determining the proportion that develop to a larval stage; the proportion of such eggs as compared with the proportion developing from normal untreated eggs is an accurate index of the degree of injury undergone.

The results of these experiments have shown that the addition of anæsthetics may have a distinct and often pronounced effect in retarding the toxic action of pure isotonic solutions of sodium and potassium salts. This protective or antitoxic effect is most readily demonstrated in those solutions where the cytolytic action is sufficiently rapid to kill all of the eggs in a comparatively brief time, *i. e.*, within one to two hours. Sodium chloride solution has this action on normal mature starfish eggs; in the presence of anæsthetics the life of the egg in the solution is decidedly prolonged (see below, page 7). On

<sup>2</sup> The reasons why mere increase of surface permeability is injurious or destructive to the cell are discussed in my earlier paper on the general biological significance of changes of permeability, in *Biological bulletin*, 1909, xvii, pp. 192 ff. The conclusion is there reached that "in general toxic action must be regarded as depending in many cases primarily on an alteration, particularly an *increase*, in the normal permeability of the cells." Further evidence that antitoxic action consists in a prevention of this increase is presented in my papers on permeability changes in relation to stimulation and the initiation of cell division, in this *Journal*, 1909, xxiv, pp. 23 ff., 486 ff., and 1910, xxvi, pp. 117 ff.

Arbacia eggs the action of sodium chloride is much more gradual, and in most of the experiments with these eggs the more rapidly acting salts, iodide, sulphocyanate, and nitrate — of both sodium and potassium — were used. Pure isotonic solutions of all these salts, with the exception of  $\text{KNO}_3$ , kill unfertilized Arbacia eggs within one and a half hours or less, sodium being distinctly more toxic than potassium; in all of these solutions various anæsthetics in appropriate concentrations decrease the rate of toxic action, *i. e.*, exert a definite antitoxic influence, as the experiments described below will illustrate. In the case of more gradually acting salt solutions, such as sodium chloride, which requires some hours to kill all of these eggs, anæsthetics have little or no antitoxic effect.

The rate of action of the salt solution is thus an important factor in determining the possibility and the degree of counteraction through anæsthetics. Apparently these substances check a rapid action, but have little effect on one more gradual. It seems probable that anæsthetics protect unfertilized Arbacia eggs against solutions of sodium iodide or potassium sulphocyanate mainly by preventing the marked and rapid increase in permeability which occurs at or shortly after the time of transfer to the pure salt solution.<sup>3</sup> In the preceding paper I have adduced evidence that in anæsthesia the plasma membranes of irritable tissues are so modified as to render more difficult a *rapid* increase in permeability; hence stimulation, which involves this kind of change, is prevented. In the case of these egg cells the conditions appear to be essentially similar; the initial rapid increase in permeability, with the associated toxic action, is checked; but the more gradual alterations in the egg following prolonged exposure to the solution take place as before. Hence, a distinct antitoxic influence is evident as a rule only during the first hour or two in the solution; later this influence ceases to be perceptible. For the same reason the toxicity of sodium chloride solutions, which act gradually on Arbacia eggs, is not perceptibly counteracted by anæsthetics. These substances thus exhibit a characteristic contrast to such a salt as calcium chloride, as illustrated by the following instance. One hour's exposure to  $m/2$  NaI typically kills all eggs; in the presence of the

<sup>3</sup> Evidence of this effect is seen in the characteristic membrane formation and initiation of cleavage produced by brief exposure to these solutions. Cf. this Journal, 1910, xxvi, p. 106; 1911, xxvii, p. 289.

most favorable concentration of chloral hydrate (0.1 to 0.5 per cent in  $m/2$  NaI) a minority of eggs — in my best experiments 20–30 per cent — may survive an exposure of two hours. Eggs left for this period in  $m/2$  NaI containing a favorable proportion of calcium chloride are only slightly injured, and all form swimming larvæ when transferred to sea water and fertilized; a fair proportion of larvæ develop from eggs fertilized even after eighteen hours in such a solution. The salt thus exerts a far more lasting antitoxic influence than the anæsthetic. The difference, however, is one of degree; in both cases the basis of the antitoxic action is a modification of the plasma membrane, as my experiments with *Arenicola* larvæ clearly indicate; but apparently a modification due to changes in the condition of the lipoids alone is much less favorable than one in which all the colloids, including the proteins, are affected.

The fact that anæsthetics prevent a rapid increase of permeability and retard toxic action is a further indication that lipoids participate in the formation of the plasma membrane, and proves that the latter cannot be regarded simply as a modified protein film. The surface film of cells must contain — in accordance with Gibbs' principle — a certain proportion of every diffusible protoplasmic constituent which has any effect in lowering the surface tension of the cell boundary; lipoids, as well as proteins and other substances (varying with the specific composition of the protoplasm), must thus enter into its composition. The proportion of lipoids to proteins no doubt varies in the plasma membranes of cells, just as it is known to vary in different tissues. Hence anæsthetics affect different cells and tissues differently. In my own experiments I have found that the antitoxic action of anæsthetics is more pronounced, and can be demonstrated after a longer stay in the solutions, in the musculature of *Arenicola* larvæ than in sea-urchin or starfish eggs. Thus ether and other anæsthetics are unable to prolong the life of unfertilized *Arbacia* eggs in sulphocyanate or iodide solutions for more than one or two hours at most; while in *Arenicola* the recovery of muscular contractility in sea water, after many hours in 0.55  $m$  NaCl containing ether, chloroform, or chlore-tone, is much more complete and rapid than after a similar stay in the pure solution. Another difference between the eggs and the larvæ is that definite antitoxic effects with chloroform or alcohol cannot (in my experience) be obtained with *Arbacia* eggs; while with *Arenicola* these

effects are well marked. These differences may be due to the existence of a higher lipid content in the plasma membranes of the contractile tissue than of the eggs. There are probably also qualitative differences of lipid content; at present what I wish to emphasize is that the existence of lipoids as essential constituents of the membranes is definitely indicated by the present experiments.

#### EXPERIMENTAL.

The experiments described below were performed at Woods Hole during the summer of 1911. The unfertilized eggs of both starfish (*Asterias forbesii*) and sea-urchins (*Arbacia punctulata*) were used. The experiments with each species of egg will be described separately.

**Experiments with starfish eggs.**—The unfertilized mature eggs of *Asterias forbesii* were used in these experiments, and the salt solution was in all cases isotonic sodium chloride (0.55 *m* NaCl). The procedure was as follows: The eggs, after removal from the animal, were left in sea water from two to three hours to allow time for maturation. Several cubic centimetres of a thick suspension of eggs were then brought into Erlenmeyer flasks of 50 c.c. capacity, the sea water was removed as far as possible with a pipette, and 50 c.c. of the solution added; after the eggs had settled to the bottom of the flask, as much as possible of the solution was withdrawn and replaced by 50 c.c. of fresh; the original small quantity of sea water introduced with the eggs is thus diluted at least a thousand times, so that its influence may be regarded as negligible. Where volatile anæsthetics were used the flasks were kept tightly corked. At intervals eggs were removed and examined in watch glasses. After remaining in the solutions for a period known to be sufficient for the pure salt solution to destroy all or nearly all of the eggs (one to two hours or more), the latter were transferred from each solution to a large quantity of sea water and washed free from salt and anæsthetic by one or more changes of sea water; spermatozoa were then added. The proportion of blastulæ developing from eggs exposed to any solution, as compared with the proportion developing from the control eggs left in sea water, was taken as index of the injurious action of the solution.

Pure isotonic solutions of sodium chloride have a rapid destructive action on mature starfish eggs, causing agglutination and rapid increase

of permeability.<sup>4</sup> In the course of one to two hours at normal summer temperature (20°-24°) the protoplasm of such eggs assumes an opaque and coagulated appearance; swelling and disintegration follow rapidly. The same changes occur in immature eggs, though less rapidly, indicating the presence of a more resistant plasma membrane previous to maturation. These changes are to be regarded as primarily dependent on an increase in the permeability of the plasma membrane. A similar cytolysis preceded by protoplasmic coagulation occurs normally in unfertilized eggs left in sea water for a period of fourteen to eighteen hours. Oxidations play an essential part in this change, since it is greatly retarded in the absence of oxygen or in the presence of cyanide.<sup>5</sup> The period during which the egg remains living and capable of developing after fertilization may thus be greatly prolonged by keeping in oxygen-free or cyanide-containing sea water. The cytolytic action of pure isotonic sodium chloride solution is also retarded by cyanide; the anticytolytic effect, however, is only moderate: in .55 *m* NaCl containing *m* 1000 KCN the great majority of eggs undergo coagulation within two to three hours. Calcium chloride has decidedly greater anticytolytic effect than cyanide. Anæsthetics in certain concentrations have a similar effect. The experiments summarized in Table I will illustrate:

Several other series of experiments gave similar results. Ether, chloroform, and chloral hydrate all showed in certain concentrations a definite and well-marked effect in retarding the cytolytic action of 0.55 *m* NaCl. Ether has a distinctly more favorable action than chloroform or chloral hydrate in the above concentrations. The two latter, while checking cytolysis, do not conserve the developmental power of the egg as ether does. Seven experiments in all were performed with chloroform in one sixth and one tenth saturated concentrations; the effects were similar to those described in the table: cytolysis was retarded at first, but the eggs on return to sea water after three hours in the solutions all failed on fertilization to form blastulæ. In two experiments with five volumes per cent ethyl alcohol a similar result was seen. The antitoxic action of ether and chloral hydrate was found to be exerted most favorably within a somewhat narrow range of concentrations, ranging in the case of ether from 0.7 vol. per cent to 0.4

<sup>4</sup> Cf. this Journal, 1911, xxvii, p. 291.

<sup>5</sup> J. LOEB: Archiv für die gesammte Physiologie, 1902, xciii, p. 59.

vol. per cent with an optimum at 0.5 or 0.6 vol. per cent, and in the case of chloral hydrate from 0.2 to 0.1 per cent, or possibly lower. Detailed descriptions of these experiments are omitted for lack of

TABLE I.

June 17. — Eggs of *Asterias forbesii*; the majority undergo apparently normal maturation. The fertilized eggs give numerous active gastrulæ. Unfertilized eggs were brought into the following solutions two hours after removal from the animals. After two and a half hours in the solutions they were transferred to sea water; after washing in sea water sperm was added.

| Solution.                                                           | Condition of eggs in solutions after <i>ca.</i> two hours.                                           | Effect of fertilization in sea water after two and one-half hours in solutions. |
|---------------------------------------------------------------------|------------------------------------------------------------------------------------------------------|---------------------------------------------------------------------------------|
| 1. 0.55 <i>m</i> NaCl.                                              | { <i>Ca.</i> 95 per cent dead and coagulated; a few remain clear.                                    | No development.                                                                 |
| 2. 100 v. 0.55 <i>m</i> NaCl + 5 v. <i>m</i> /2 CaCl <sub>2</sub> . | All eggs clear and normal-looking.                                                                   | Majority form blastulæ, largely abnormal.                                       |
| 3. 0.55 <i>m</i> NaCl + 0.3 per cent chloral hydrate.               | Great majority dead and coagulated as in Solution 1.                                                 | No blastulæ.                                                                    |
| 4. 0.55 <i>m</i> NaCl + 0.6 v. per cent ether.                      | { Majority coagulated, but a good many remain clear.                                                 | <i>Ca.</i> 10 per cent of mature eggs form blastulæ, largely abnormal.          |
| 5. 0.55 <i>m</i> NaCl + 0.4 v. per cent ether.                      | { Most coagulated, but clear eggs more numerous than in Solution 4.                                  | <i>Ca.</i> 20-30 per cent of mature eggs form blastulæ.                         |
| 6. 0.55 <i>m</i> NaCl + 1/6 saturated chloroform                    | { <i>Ca.</i> 50 per cent are translucent without membranes; remainder with membranes and coagulated. | No blastulæ.                                                                    |
| 7. 0.55 <i>m</i> NaCl + 1/10 saturated chloroform.                  | Great majority coagulated; a few remain clear.                                                       | Almost all die early; one blastula seen.                                        |
| 8. 0.55 <i>m</i> NaCl + <i>m</i> /1000 KCN.                         | <i>Ca.</i> 60 per cent remain clear; rest coagulated.                                                | { <i>Ca.</i> 5 per cent of mature eggs form abnormal blastulæ.                  |

space. In one series in which eggs were fertilized after two hours in the solutions, most of the mature eggs which had been exposed to 0.55 *m* NaCl containing 0.75, 0.6, and 0.5 vol. per cent ether formed blastulæ; 0.4 and 0.3 vol. per cent solutions were less favorable,

though still distinctly effective; 0.2 vol. per cent had only slight effect. In the pure 0.55 *m* NaCl almost all of the eggs were dead and coagulated after two hours. Chloral hydrate showed well-marked protective action in 0.2 per cent, but not in stronger solutions. These results are typical. In five series of experiments with ether, in concentrations ranging from 0.75 vol. per cent to 0.2 vol. per cent, the most favorable antitoxic effects were seen in concentrations between 0.6 and 0.45 vol. per cent. With chloral hydrate the best concentrations were 0.2 or 0.1 per cent (four series ranging from 0.6 to 0.1 per cent). In sea-urchin eggs also chloral hydrate was found to act most effectively in low concentrations (0.1 to 0.05 per cent; see below).

Toward the end of June the starfish eggs began to exhibit abnormal behavior: the eggs even after maturation often showed an abnormally high resistance toward 0.55 *m* NaCl; such eggs also failed to undergo the normal coagulative change in sea water and were difficult to fertilize; the action of anæsthetics was also abnormal. The behavior of these eggs will not be considered in the present paper.

**Experiments with Arbacia eggs.** — In the experiments with unfertilized eggs of *Arbacia* the chief salts used were sodium and potassium iodide, sulphocyanate and nitrate. A few series of experiments were also performed with neutral and alkaline solutions of sodium chloride. In pure neutral 0.55 *m* NaCl, with an exposure of about three hours, there was no evident antitoxic action with ether (0.6 per cent), chloroform (one sixth saturated), ethyl urethane (0.3 per cent), chloretone (one tenth and one twentieth saturated), and chloral hydrate (0.1 and 0.05 per cent). On the other hand, calcium chloride (*m*/40) and potassium cyanide (*m*/1000) showed definite and well-marked action, particularly the former. Three hours' exposure to pure 0.55 *m* NaCl typically renders most eggs incapable of development, but a considerable proportion may survive; the toxic action of this salt is thus comparatively gradual, — hence, in all probability the absence of protective action with anæsthetics as explained above. The addition of alkali (*m*/500 NaOH) to the 0.55 *m* NaCl increases the toxicity of the solution, apparently by accelerating its permeability-increasing action; and in such alkaline solutions chloral hydrate and chloretone, and to a less degree ether, were found to exhibit well-marked antitoxic action. It is remarkable that calcium, so efficacious with the neutral solution, *increases* the toxicity of the alkaline solution. Otherwise

the results of these experiments correspond closely with those obtained with the more rapidly acting salts, as described below. The experiments with solutions of the other salts named above will now be described in order.

TABLE II.

July 20, 1911. — Unfertilized eggs of *Arbacia punctulata* were exposed to the following solutions for one and three-quarters hours; they were then transferred to sea water and sperm was added.

| Solution.                                           | Result (condition after sixteen hours).                                                |
|-----------------------------------------------------|----------------------------------------------------------------------------------------|
| 1. $m/2$ NaI.                                       | No development; eggs dead and partly decolorized.                                      |
| 2. 9 vols. $m/2$ NaI + 1 vol. $m/2$ $\text{CaCl}_2$ | Most eggs form blastulæ, largely irregular; many surface swimmers.                     |
| 3. $m/2$ NaI + $m/1000$ KCN.                        | Almost all are dead; largely disintegrated; only one blastula seen.                    |
| 4. $m/2$ NaI + 0.6 v. per cent ether.               | All dead and laked.                                                                    |
| 5. $m/2$ NaI + 0.2 per cent urethane.               | A few blastulæ — less than 1 per cent.                                                 |
| 6. $m/2$ NaI + 0.1 per cent urethane.               | A few blastulæ — less than 1 per cent.                                                 |
| 7. $m/2$ NaI + 0.05 per cent urethane.              | A few blastulæ; somewhat more than in Experiments 5 and 6.                             |
| 8. $m/2$ NaI + $1/8$ saturated chloretone.          | A few blastulæ.                                                                        |
| 9. $m/2$ NaI + $1/16$ saturated chlorotone.         | A few blastulæ — less than 1 per cent.                                                 |
| 10. $m/2$ NaI + 0.1 per cent chloral hydrate.       | A fair number of blastulæ — more than in Experiments 5 to 9 — <i>ca.</i> 3-4 per cent. |

*Sodium iodide.* — In solutions of this salt antitoxic effects were obtained with urethane, chloretone, and chloral hydrate, but not with ether or chloroform. The action of  $m/2$  NaI is not readily counteracted, and the antitoxic effects with anæsthetics are relatively slight; in four out of eight series of experiments the anæsthetics showed no definite protective action. On the other hand, calcium and to a less degree cyanide are always highly effective. Table II summarizes the results of a favorable series of experiments.

In a second series on July 21 with ether (0.8, 0.6, and 0.5 vol. per cent) and chloral hydrate (0.1 and 0.05 per cent) no definite antitoxic



action was seen with ether, but with chloral hydrate this action was well marked; after two hours in the solutions of this anæsthetic, followed by return to sea water and fertilization, a considerable proportion of eggs — from 30 per cent to 40 per cent — formed blastulæ. Pure  $m/2$  NaI — Kahlbaum's salt, dissolved shortly before using so as to be free from iodine — as a rule kills all of the eggs within an hour, though occasionally a few eggs may survive one and a half or even two hours' exposure. The above is the most decided antitoxic action shown by an anæsthetic in any of my experiments with this salt. Calcium is far more effective; in the above series almost all eggs formed blastulæ after two hours in a mixture of 9 vols.  $m/2$  NaI *plus* 1 vol.  $m/2$   $\text{CaCl}_2$ ; in another series a few eggs formed blastulæ after eighteen hours in the same mixture. Cyanide is decidedly less effective than calcium, though its action is perfectly distinct; in no case, however, did it prove so effectual as chloral hydrate in the experiments just cited.

*Sodium sulphocyanate.* — Two series of experiments were performed with this salt. In the first series all of the eggs failed to develop after an exposure of one hour and five minutes to pure  $m/2$  NaCNS;<sup>6</sup> while nearly all of those in the calcium-containing (*plus*  $m/20$   $\text{CaCl}_2$ ) and about half of those in the cyanide-containing (*plus*  $m/1000$  KCN) solutions formed blastulæ. On the other hand, ether (0.8 and 0.6 vol. per cent), urethane (0.4 and 0.2 per cent), chloretone (one tenth saturated), and chloral hydrate (0.1 and 0.05 per cent), while retarding cytolysis, did not enable the eggs to withstand this exposure. In the second series, with exposures of thirty minutes, urethane, chloretone, and especially chloral hydrate showed distinct protective action; with ether the effect was doubtful. A few eggs survived this exposure to the pure solution; the proportion of survivors was decidedly increased in the presence of the above anæsthetics. The extraction of pigment was distinctly retarded in those solutions where antitoxic action was evident, especially in those containing calcium and cyanide — indicating again that the antitoxic effect runs parallel with the prevention of abnormal increase of permeability.

*Sodium nitrate.* — Four series of experiments were performed with  $m/2$   $\text{NaNO}_3$  with respective exposures of twenty minutes, one and a

<sup>6</sup> The salt was of Kahlbaum's make and contained some alkali. The solutions were rendered neutral to phenolphthalein before using.

quarter hours, two hours five minutes, and three hours ten minutes. In the series with three hours' exposure no antitoxic action was apparent except with calcium and cyanide. With two hours' exposure chloral hydrate (0.1 and 0.05 per cent), chloretone (one tenth and one twentieth saturated), and urethane (0.4 and 0.2 per cent) showed distinct action; all eggs were destroyed in the pure  $m/2$   $\text{NaNO}_3$ , while a considerable number survived and yielded larvæ in the presence of the anæsthetic, especially with 0.2 per cent urethane (40 to 50 per cent blastulæ) and one tenth saturated chloretone (30 to 40 per cent blastulæ). Ether (0.6 vol. per cent) showed no antitoxic action. Calcium and cyanide were markedly effective, as usual with sodium salts. The protective action was plainly correlated with a prevention of the increase of permeability as indicated by exit of pigment. Results essentially similar to the above were obtained in the other two series. In one experiment a few eggs survived an exposure of nineteen hours to  $m/2$   $\text{NaNO}_3$  containing 0.1 per cent urethane. Only cyanide and calcium showed a comparable action. Ether showed a slight protective action in one experiment, but chloroform none.

*Potassium salts.* — In general, potassium salts in pure isotonic solution are decidedly less toxic to unfertilized Arbacia eggs than the corresponding sodium salts. Anæsthetics show definite antitoxic action with the iodide and sulphocyanate. Potassium nitrate is comparatively non-toxic; in two experiments a considerable number of eggs which had been exposed for nineteen hours to  $m/2$   $\text{KNO}_3$  formed larvæ on fertilization; in correspondence with this slowness of action the antitoxic effects with anæsthetics are less distinct with nitrate than with the other two salts.

*Potassium iodide.* — Three separate series of experiments were performed with  $m/2$   $\text{KI}$  with exposures of one hour forty minutes, two hours fifteen minutes, and three hours, respectively. Table III gives the results of the second of these series.

The series with exposures of one hour and forty minutes gave an almost identical result except that the results with urethane were more favorable. The same solutions were used, except that 0.8 per cent ether was substituted for one twentieth saturated chloretone. The series with three hours' exposure also showed distinct antitoxic action with chloral hydrate and chloretone, but doubtful action with

urethane; the eggs exposed to the pure solution for this period gave less than 1 per cent of blastulæ; the proportion of blastulæ from eggs exposed to the anæsthetic-containing solutions was also small but dis-

TABLE III.

July 31, 1911. — Unfertilized eggs of *Arbacia* were exposed to the following solutions for two hours and fifteen minutes, then returned to sea water and fertilized.<sup>1</sup>

| Solution.                                                                                                                                                                                                                                                                                                                                                      | Result (condition after nineteen hours).                                              |
|----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|---------------------------------------------------------------------------------------|
| 1. $m/2$ KI.                                                                                                                                                                                                                                                                                                                                                   | About 50 per cent form blastulæ.                                                      |
| 2. 9 vols. $m/2$ KI + 1 vol. $m/2$ $\text{CaCl}_2$ .                                                                                                                                                                                                                                                                                                           | Proportion of blastulæ somewhat greater than in Experiment 1.                         |
| 3. $m/2$ KI + $m/1000$ KCN.                                                                                                                                                                                                                                                                                                                                    | All dead and coagulated.                                                              |
| 4. $m/2$ KI + 0.6 vol. per cent ether.                                                                                                                                                                                                                                                                                                                         | All dead and coagulated.                                                              |
| 5. $m/2$ KI + 0.4 per cent urethane.                                                                                                                                                                                                                                                                                                                           | Ca. 40-50 per cent form blastulæ; rather less favorable than Experiment 1.            |
| 6. $m/2$ KI + 0.2 per cent urethane.                                                                                                                                                                                                                                                                                                                           | Ca. 50 per cent form blastulæ; surface swimmers more numerous than in Experiment 1.   |
| 7. $m/2$ KI + 1/10 saturated chlore-tone.                                                                                                                                                                                                                                                                                                                      | Marked improvement; 90 per cent or more eggs form blastulæ; better than Experiment 2. |
| 8. $m/2$ KI + 1/20 saturated chlore-tone.                                                                                                                                                                                                                                                                                                                      | Marked improvement; like Experiment 7.                                                |
| 9. $m/2$ KI + 0.1 per cent chloral hydrate.                                                                                                                                                                                                                                                                                                                    | Improvement over Experiment 1, though less favorable than Experiments 7 and 8.        |
| 10. $m/2$ KI + 0.05 per cent chloral hydrate.                                                                                                                                                                                                                                                                                                                  | Ca. 90 per cent form blastulæ; essentially like Experiments 7 and 8.                  |
| <sup>1</sup> After ca. twenty hours in the solutions the eggs were found completely laked in Solutions 1, 3, and 4; partly laked in Solutions 5 and 6; while pigment was retained in Solutions 2, 7, 8, 9, and 10. The antitoxic action thus shows a general parallelism with the action in preventing increase of permeability of the egg to its own pigment. |                                                                                       |

tinctly higher — from 3 to 5 per cent. It is noteworthy that in all three series cyanide showed no protective action, but, on the contrary, increased the toxicity of the solution. The same was true of ether. Calcium chloride in all cases proved much less effective with this salt than with sodium iodide.

*Potassium sulphocyanate.* — With this salt seven series of experiments were performed, the results of which showed close agreement.

The periods of exposure ranged from forty-five minutes to three hours. Exposures of one hour twenty-five minutes and one hour forty minutes to pure  $m/2$  KCNS killed all the eggs; a few survived exposures of one hour (ca. 30 per cent formed blastulæ), one hour five minutes (ca. 5 per cent blastulæ), one hour ten minutes (ca. 10 to 15 per cent blastulæ), and one hour fifteen minutes, (ca. 2-3 per cent blastulæ); and about half the eggs developed to blastulæ after an exposure of forty-five minutes to the pure solution.

Table IV summarizes the results of a series of experiments in which eggs were transferred to sea water and fertilized after one, two, and three hours' exposure to the solutions.

The results of the other series of experiments agreed essentially with the above. Chloroform showed no protective action in any experiment; alcohol also proved ineffective. Ether and especially chloral hydrate showed marked antitoxic effectiveness in certain concentrations; the optimum for chloral hydrate was 0.1 to 0.05 per cent; the above result was the best obtained with ether. Ethyl urethane, in a series of experiments with this anæsthetic in the concentrations 0.4, 0.3, 0.2, and 0.1 per cent, also exhibited marked antitoxic action in solution of this salt. After one hour in pure  $m/2$  KCNS, from 10 to 15 per cent of eggs formed blastulæ on fertilization, while of the eggs exposed to the same solution containing 0.4, 0.3, and 0.2 per cent urethane, from 75 to 90 per cent formed active blastulæ; in the 0.1 per cent solution there was no distinct antitoxic action. Chloretone was also used in this series, in concentrations of one tenth, one fifteenth, and one twentieth saturated, but showed no definite effects.

In a second similar series, with ether (0.6 vol. per cent), urethane (0.3 and 0.2 per cent), and chloretone (one tenth, one twentieth, and one thirtieth saturated), and exposures of one hour forty minutes, none of the eggs reached a larval stage; this exposure was evidently too long.

It is again to be noted that with this salt, as with potassium iodide, calcium proved decidedly less effective as antitoxic agent than with the corresponding sodium salt; also that potassium cyanide increased rather than decreased the toxicity of the solution.

*Potassium nitrate.* — Solutions of this salt are decidedly less toxic than those of iodide and sulphocyanate, and in the four series of ex-

TABLE IV.

July 7, 1911. — Unfertilized eggs of *Arbacia* were placed in the following solutions. Portions were transferred to sea water after respectively one, two, and three hours in the solutions; to each lot sperm was then added. The condition of the eggs next day is indicated in the table.

| Solution.                                               | Eggs exposed to solutions one hour.                    | Eggs exposed to solutions two hours.                                                                             |
|---------------------------------------------------------|--------------------------------------------------------|------------------------------------------------------------------------------------------------------------------|
| 1. .55 <i>m</i> KCNS.                                   | { About one third form mostly irregular blastulæ.      | All dead and coagulated.                                                                                         |
| 2. 9 vols. .55 <i>m</i> KCNS + 1 vol. <i>m</i> /2 CaCl. | Great majority form blastulæ.                          | { About 75 per cent form blastulæ [of eggs exposed three hours very few form blastulæ].                          |
| 3. .55 <i>m</i> KCNS + <i>m</i> /1000 KCN.              | Few blastulæ — <i>ca.</i> 2-4 per cent.                | All dead.                                                                                                        |
| 4. 55 <i>m</i> KCNS + 0.8 vol. per cent ether.          | Great majority form blastulæ.                          | Nearly all dead; <i>ca.</i> 1 per cent blastulæ.                                                                 |
| 5. .55 <i>m</i> KCNS + 1 v. per cent ether.             | A few blastulæ — <i>ca.</i> 3-4 per cent.              | All dead.                                                                                                        |
| 6. .55 <i>m</i> KCNS + 1/6 saturated chloroform.        | All dead and coagulated.                               | All dead.                                                                                                        |
| 7. .55 <i>m</i> KCNS + 1/8 saturated chloroform.        | All dead.                                              | All dead.                                                                                                        |
| 8. 55 <i>m</i> KCNS + 5 vol. per cent ethyl alcohol.    | A few blastulæ — less than 1 per cent.                 | All dead.                                                                                                        |
| 9. .55 <i>m</i> KCNS + 0.2 per cent chloral hydrate.    | A few blastulæ — <i>ca.</i> 2-3 per cent.              | A few blastulæ — <i>ca.</i> 2 per cent [eggs exposed three hours all dead].                                      |
| 10. .55 <i>m</i> KCNS + 0.1 per cent chloral hydrate.   | From 35 to 50 per cent form mostly irregular blastulæ. | { <i>Ca.</i> 20-25 per cent form blastulæ [eggs exposed three hours give a few blastulæ — less than 1 per cent.] |

periments tried the anæsthetics showed little antitoxic action. The following series (Table V), with an exposure of two hours, shows definite action with chloral hydrate, urethane, and chloretone. A few eggs exposed for twenty hours to solutions containing 0.2 per cent

urethane and one twentieth saturated chloretone survived and yielded larvæ on fertilization, while none of those similarly exposed to the pure solution developed.

TABLE V.

July 18, 1911. — Unfertilized eggs of *Arbacia* were placed in the following solutions. Eggs were transferred to sea water after periods of two and twenty hours and fertilized. The results were as follows.

| Solution.                                          | Result (condition the day after fertilization).<br>Two hours' exposure.                  | Result (condition the day after fertilization).<br>Twenty hours' exposure. |
|----------------------------------------------------|------------------------------------------------------------------------------------------|----------------------------------------------------------------------------|
| 1. $m/2$ $KNO_3$ .                                 | From half to two thirds form blastulæ.                                                   | All dead and coagulated.                                                   |
| 2. 9 vols. $m/2$ $KNO_3$ + 1 vol. $m/2$ $CaCl_2$ . | Essentially like Experiment 1.                                                           | All dead.                                                                  |
| 3. $m/2$ $KNO_3$ + $m/1000$ KCN.                   | 5-10 per cent form blastulæ.                                                             | All dead.                                                                  |
| 4. $m/2$ $KNO_3$ + 0.6 vol. per cent ether.        | { Majority dead; <i>ca.</i> 20-25 per cent form blastulæ.                                | All dead.                                                                  |
| 5. $m/2$ $KNO_3$ + 0.1 per cent chloral hydrate.   | { More favorable than Experiment 1; <i>ca.</i> 70 per cent to 85 per cent form blastulæ. | All dead.                                                                  |
| 6. $m/2$ $KNO_3$ + 0.05 per cent chloral hydrate.  | { Like Experiment 5.                                                                     | All dead.                                                                  |
| 7. $m/2$ $KNO_3$ + 0.4 per cent urethane.          | { Great majority form blastulæ — <i>ca.</i> 85 per cent.                                 | All dead.                                                                  |
| 8. $m/2$ $KNO_3$ + 0.2 per cent urethane.          | <i>Ca.</i> 70 per cent to 80 per cent form blastulæ.                                     | { A small proportion form blastulæ — <i>ca.</i> 1 to 2 per cent.           |
| 9. $m/2$ $KNO_3$ + 1/10 saturated chloretone.      | Almost all (more than 90 per cent) form blastulæ.                                        | All dead.                                                                  |
| 10. $m/2$ $KNO_3$ + 1/20 saturated chloretone.     | Almost all form blastulæ.                                                                | { A small proportion form blastulæ — <i>ca.</i> 1 per cent.                |

The experiments with potassium nitrate again illustrate the comparative ineffectiveness of calcium as antitoxic agent with potassium as compared with sodium salts; also the unfavorable action of potas-

sium cyanide in solutions of potassium salts. This contrast between sodium and potassium salts has appeared through all of my experiments with unfertilized *Arbacia* eggs. Pure solutions of potassium salts are characteristically less toxic than those of the corresponding sodium salts; but in the presence of a moderate proportion of calcium chloride the relations are reversed. Sodium salts appear to be distinctively characterized by the readiness with which the toxicity of the pure solutions may be decreased by the addition of calcium; while in solutions of potassium salts the antitoxic action of calcium is relatively slight. Somewhat similar conditions are exhibited by *Arenicola* larvæ, which also withstand prolonged exposure to  $m/2$  KCl better than to  $m/2$  NaCl; calcium chloride has a markedly antagonistic action to sodium chloride, but relatively slight to potassium chloride.<sup>7</sup> Cyanide also shows a remarkable difference in its action on unfertilized *Arbacia* eggs in solutions of sodium as compared with potassium salts. The immediate toxic action of sodium salts is decreased in the presence of  $m/1000$  KCN, while that of potassium salts is distinctly and often markedly increased. I am unable at present to assign any grounds for this difference; possibly it indicates that sodium and potassium salts act primarily on different constituents of, or on different processes in, the plasma membrane. Loeb has found that the toxic action of many substances and agencies<sup>8</sup> upon fertilized sea-urchin eggs is retarded by cyanide, and he has referred the antitoxic action in such cases to a suppression of abnormal or destructive oxidation processes. If the toxic action of salt solutions is due to the abnormal changes which they produce in the plasma membrane, the above facts seem to indicate that oxidations are in some manner associated with changes in the permeability of the membrane. Suppression of oxidative processes prevents pure solutions of sodium salts from increasing the permeability of the plasma membrane as they would otherwise do, and hence diminishes the toxicity of these solutions. But why cyanide fails to exercise this influence in solutions of potassium salts remains unexplained on any such hypothesis. It must be recognized that toxic effects may be the expression of a variety of alterations in th

<sup>7</sup> Cf. this Journal, 1911, xxviii, p. 213.

<sup>8</sup> Neutral salt solutions, hyperalkaline solutions, sugar solutions, hypertonic and hypotonic solutions, narcotics. Cf. J. LOEB: *Biochemische Zeitschrift*, 1910, xxix, p. 80.

living system. Hence an antitoxic agency which is effective with one form of toxic action may be quite ineffective with another. Further consideration of this question is deferred for the present.

#### SUMMARY.

The main facts and general conclusions of the foregoing paper may be briefly summarized as follows:

1. The permeability-increasing and cytolytic action of isotonic solutions of neutral sodium and potassium salts on unfertilized starfish and sea-urchin eggs is retarded in the presence of various anæsthetics in certain definite concentrations. The period during which the eggs remain living in the salt solutions, and capable of development after fertilization, may thus be greatly prolonged. This protective or anti-toxic influence is comparable to that exercised by calcium or magnesium salts, though as a rule it is less marked.
2. The view that lipoids enter into the formation of the plasma membrane thus receives confirmation. Evidently the state of the lipoids determines the readiness with which the membrane undergoes alteration. The conditions suggest that the lipoids have a "protective" relation to the other colloids of the membrane, limiting or preventing changes of aggregation state in these latter, and that during anæsthesia this influence is increased.
3. Calcium chloride is much less effective as antitoxic agent with potassium than with sodium salts.
4. Potassium cyanide in  $m/1000$  concentration, while decreasing the immediate toxic action of sodium salts on sea-urchin eggs, increases that of potassium salts.









## THE PHYSIOLOGICAL SIGNIFICANCE OF THE SEGMENTED STRUCTURE OF THE STRIATED MUSCLE FIBRE

THE question of the physiological significance of the segmented structure of striated muscle fibers remains for most physiologists one of the standing enigmas of their science. What relation—if any—has this structure to the power of rapid and instantly reversible contraction which is the distinctive peculiarity of this tissue? No entirely satisfactory answer to this question has hitherto been found; those which have been proposed are as diverse as their authors' conceptions of the ultimate structure of the tissue. Perhaps the chief root of the difficulty lies here. The histological literature is full of contradictions and hence—since all can not be right—of misinterpretations. Before agreement can be reached on the physiological question, it is evident that a clear and satisfactory conception of the essential structure of the living muscle-cell is necessary. Many of the structural minutiae visible in histological preparations vary according to the nature of the treatment accorded the tissue. Their physiological significance is thus doubtful. During recent years a certain change in the procedure of investigators has become apparent. Experience of the readiness with which the structure or "aggregation-state" of a colloidal system may be altered has made it clear that such structures are not always to be regarded as preexistent in the living tissue. They are rather to be regarded as appearances from which, on the basis of an adequate knowledge of the behavior of colloidal systems under similar treatment, inferences may be drawn as to the original disposition and state of the colloidal material in the living system. Inferences so drawn require to be controlled by an exact knowledge of the structural appearances in living muscle during both rest and contrac-

tion. Hence recent investigators—as Hürthle and Meigs—have relied mainly on direct and photographic observation of living muscle fibers. But even results so gained show considerable disagreement in detail, and unfortunately they have proved compatible with diametrically opposed conceptions of the essential nature of the contractile process.

Certain definite conclusions have, however, been reached. It is agreed that the contractile elements are solid fibrils—consisting supposedly of water-swollen myosin—which are embedded in a more fluid sarcoplasm; the fibrils are not optically homogeneous, but exhibit a regular alternation of longer segments consisting of more refractive and largely doubly refractive (anisotropic) material, with shorter less refractive segments showing little or no double refraction (isotropic). In the voluntary muscle-cell of vertebrates the fibrils are crowded together closely, and in such a manner that the adjacent anisotropic and isotropic segments of different fibrils lie at the same level; this level is perpendicular to the long axis of the muscle cell, hence the latter, as a whole, shows the characteristic cross-striation. It is this peculiarity of parallelism in the disposition of the fibrillar segments which Hürthle characterizes as "schwer verständlich." It plainly suggests that the fibrils are laterally conjoined in a definite manner so as to form a system coherent throughout the cell. Conceptions differ, however, as to the ultimate structure of the individual fibrils, and particularly as to the nature of the conditions producing the segmented appearance.

I shall not attempt in this place to discriminate minutely between conflicting views regarding structure; my aim is merely to show that a segmented structure is in itself—

and largely irrespective of the precise nature of the structural conditions that determine the segmentation—a condition favorable to rapid and quickly reversible changes of form. The questions to be discussed are thus: What mechanical advantage does a rapidly contractile colloidal system like muscle derive (1) from having its fibrils regularly and minutely segmented, and (2) from having the corresponding segments of adjacent fibrils at the same level?

Considered from a physico-chemical point of view, the individual muscle-fibril forms a colloidal system in which regions showing a well-marked contrast in optical and apparently also in chemical properties (evidence from staining) alternate regularly with one another. It is, however, doubtful if the alternate segments differ in their essential chemical constitution; the evidence seems rather to indicate that the same colloidal material forms the solid substratum of the fibril throughout its entire length, but that this material differs in its state of aggregation in alternate segments. The colloidal particles must be regarded as forming a coherent system throughout the entire fibril, as in a gel; otherwise the fibril would have no tensile strength. Between the coherent particles of any gel are interstitial fluid-containing spaces.<sup>1</sup> If the fibril is essentially a gel, as thus assumed, with myosin as the chief colloid, its physical condition from segment to segment can vary only in the concentration and state of aggregation of its colloid material. There are indications that the colloidal particles (probably submicrons) are more densely aggregated in the dim bands and less densely in the light; in this case the interstitial spaces must be smaller in the dim and larger in the light

<sup>1</sup> The recent observations of Bachmann, made in Zsigmondy's laboratory, on the ultramicroscopic structure of gels, show that during gelation the motion of the submicrons changes from one of a free translatory character to one in which the submicrons undergo only slight vibratory movements about fixed positions of equilibrium. There is thus in gelation an aggregation of submicrons and amicrons to form a coherent system, with fluid-containing interspaces. Cf. *Zeitschrift für anorganische Chemie*, 1911, p. 125.

bands; i. e., the proportion of displaceable fluid material is greater in the light bands, the latter, so to speak, having the looser texture of the two. Such a conception explains many characteristic observations, such as the beaded form shown by fibrils under certain conditions; the greater compressibility of the isotropic segments (indicating a greater fluidity), as shown by the experiments of Haycraft, who obtained impressions of the segmented structure by pressing living fibers against collodion; the facts that the double refraction appears rather to diminish than entirely to disappear in the light bands, and that adsorbed coloring materials, such as hæmatoxylin, though taken up by the whole fibril, are extracted most readily from the isotropic segments, just as though the adsorbing surface were there relatively less. Hürthle also compares the material composing the fibril to a gel; he regards this as chemically homogeneous throughout, but as differing in its physical condition in alternate segments. He adduces the analogy of the nodes in a stretched vibrating string, implying that the differences between the alternating segments are purely physical and independent of differences in chemical composition. Although it is doubtful that marked differences in the colloidal aggregation-state could exist between adjacent segments without at least some quantitative differences of chemical composition due to differences of adsorption, etc., yet the essential conception of the fibril as essentially homogeneous in its chemical composition is not altered by recognizing the existence of a segmented structure of the above conceived kind.

On this view the fibril is to be regarded as a column of colloidal material having the essential properties of a gel—i. e., a system in which the colloidal particles cohere; the particles, however, are not homogeneously distributed in this gel, but are relatively densely aggregated in the anisotropic segments and loosely in the isotropic; in the latter the interstitial fluid-containing spaces are therefore relatively larger. It should be noted that in all muscles the isotropic segments are shorter than the anisotropic; also that the best photo-

graphic evidence indicates that the actual shortening is confined to the anisotropic regions of the fibril, *i. e.*, to the regions where the colloidal particles are the most closely aggregated. The significance of this will be apparent later.

The considerations urged in the preceding paragraph relate to the individual fibril and do not explain the lateral coherence of the fibrils. It seems clear, from the fact that the striation is preserved during contraction, that transverse connections must exist between adjacent fibrils, otherwise the latter would certainly undergo relative displacement more frequently than observation shows to be the case. But the histological evidence of such cross connections is imperfect, although the view seems well founded that the appearances known as Hensen's and Krause's lines (*M* and *Z* lines) correspond to regions where adjacent fibrils are laterally conjoined. This view is supported by Heidenhain on the basis of numerous observations on fixed muscle of various kinds; and a continuity of the *Z*-lines from fibril to fibril, even when the latter are separated by some distance, is clearly apparent in some of Meigs's photographs. Both of these appearances, especially the *Z* or intermediate line, have been interpreted as membranes subdividing the fibrils at segmental intervals; but they seem to lack the continuity which such a conception demands. A continuous membrane would show definite optical appearances due to reflection of light at its surface. The so-called *J*-lines, which suggest such reflection and hence support this conception, are variable and often unapparent. On the other hand, the existence of narrow cross-connections between adjacent fibrils would undoubtedly account for the observed appearances. I am, therefore, inclined to favor this interpretation. According to this conception these structures are of no essential importance in contraction except in so far as they prevent relative displacement of adjacent fibrils. But such displacement, if permitted, would interfere with the contractile properties of the system, as I shall show later, so that the physiological rôle thus assigned to these structures may after all be in-

dispensable. This view is however quite opposed to any hypothesis—like that of Pütter—which regards the intermediate lines as corresponding to membranes whose state of permeability determines the degree of osmotic distension of the muscle segments, and so the state of contraction. The evidence of their membrane character seems insufficient to serve as support for such a speculative view as this. On the other hand, the lateral coherence of the fibrils is an undoubted fact which must have a structural basis, and direct observations exist which indicate that at least the *Z* lines—which appear to be the more constant of the two—do in fact cross the intervals between the fibrils. Structures thus continuous from fibril to fibril are most naturally interpreted as connectives.

We may now consider the physiological problem as to the nature of the essential physical changes which form the direct condition of the characteristic mechanical deformation of active muscle. The precise nature of the energy-yielding metabolic process need not concern us here. As well known, various more or less seriously conflicting hypotheses exist. There is considerable evidence of a displacement of fluid within the contractile elements during activity, and this fact has led to the development of theories which assign to this transfer of fluid the essential rôle in the process of contraction. Thus Engelmann and many others have referred the process to a water-absorption or swelling of certain structural elements—just as gelatine sheets swell in water, and more rapidly when the water is warm or acidulated than when it is cold or neutral. The general structural conception put forward some time ago by McDougall, and recently favored by Meigs and others, has been that of a tissue composed of elements comparable to somewhat elongated or spindle-shaped fluid-containing sacs with inextensible walls; these elements on distension approach a spherical form, with consequent approximation of their opposite ends. A certain degree of shortening (about 37 per cent.) may thus theoretically be accounted for. That the actual shortening often greatly exceeds this proportion is unfavorable to such

hypotheses, though perhaps not necessarily incompatible with them. The structural conditions might conceivably be such that the swelling elements at their maximal normal distension adopt a form in which the ratio of transverse to longitudinal diameters—assuming these to correspond with those of the muscle-cell—is increased sufficiently to account for a much greater degree of shortening than the above. All that would be necessary to render such a hypothesis adequate in this respect would be to assign a certain definite structure and form to the elements. Take for instance the case of a tissue composed of structural units resembling the extended elaters of the spores of *Equisetum*; as is well known, these structures when slightly moistened wind themselves closely around the spore; the total diameter of the system, spore *plus* elaters, may thus be reduced to a small fraction of the original diameter as measured between the tips of the extended elaters. One might conceive of muscle as composed of elements similar in contractile properties to elaters, united in a definite manner to form a contractile system; and it would no doubt be possible, by exercising some ingenuity, to reconcile such a conception with the main histological appearances. Hypotheses that refer the contraction to swelling of the contractile elements are thus not to be dismissed by advocates of other views as inadmissible on the ground of purely geometrical considerations. The objections to this type of explanation are of quite another nature; and since they are in my opinion sufficiently weighty to render it extremely doubtful that this kind of physical change could ever form the basis of a movement so rapid, responsive and quickly reversible as muscular contraction, I shall briefly recapitulate what I consider to be the chief inadequacies of such hypotheses.

(1) The time required for a contraction and relaxation due to swelling-changes in the colloidal contractile elements—involving both the incorporation of water into the colloid and its release—seems to be too great. Pauli, indeed, once estimated that if the elements have the swelling properties of gelatine discs, and the same surface-volume ratio as the

muscle-segments, the rate of swelling might be sufficient to account for a contraction as rapid as that of frogs' muscle. But the single twitch may be many times shorter than this, as in insects' wing-muscle, where moreover the muscle-segments are larger than in vertebrate muscle. It is of course possible to reply to this objection that the actual elements concerned may be much smaller than the visible muscle-segments. Still, in any case, since the single-twitch curve of striated muscle is symmetrical, the rate of the water-absorption would have to correspond in its time-relations with that of the water-loss. These curves, however, have been shown to follow different courses in those cases which have been actually investigated (by van Bemmelen). (2) A more serious difficulty is that the temperature-coefficient of the mechanical energy of contraction, according to Bernstein's investigations, is *negative*; i. e., within a normal range—up to 30°—the lifting power of the twitch is *increased*, with a given intensity of stimulus, by lowering the temperature. The temperature-coefficient of swelling processes is however positive and large, like that of chemical reactions; that of surface tension, on the contrary, is negative. Bernstein's experiments must be regarded as very significant, since the temperature-coefficients of the chemical changes concerned in contraction are of course positive; the above result would seem therefore quite unaccountable if a chemical change, like the production of acid, preceded and formed the condition of the contractile change. These experiments thus appear to indicate, first, that the process immediately conditioning the contraction is only indirectly dependent on a chemical change,<sup>3</sup> and, second, since this process has a negative temperature-coefficient (a distinctive peculiarity of surface-tension), that a change of surface-tension in the ultimate contractile elements is the direct source of the energy of contraction. (3) A further disadvantage of the "swelling-hypotheses"—as contrasted with the surface-

<sup>3</sup> Resembling in this respect the plant-movements due to changes in the permeability of the plasma-membranes of turgid cells (in *Mimosa*, *Dionaea*, etc.).

tension hypothesis—is that they offer no suggestion as to the nature of the connection between the electrical variation accompanying contraction and the actual contractile process. In electrical stimulation a change in the electrical polarization of the plasma-membrane is almost certainly the essential or critical event. If the membrane enclosing a colloidal system, such as a muscle-cell, changes its polarization, a corresponding change of polarization must occur at *all* of the electrically polarized surfaces within the system thus enclosed,\* including presumably the surfaces of the colloidal particles composing the contractile elements. Changes of electrical polarization at surfaces are definitely known to alter the surface-tension. On the other hand, the relation assumed to exist between the polarization-change of stimulation and the swelling of the colloidal elements, according to the hypothesis under consideration, must be exceedingly indirect. A chemical change must first be assumed to occur, producing substances, supposedly acid, which increase the swelling properties of the colloid. There is nothing unreasonable in this view, but it fails to suggest any explanation of the close parallelism which exists between the electrical and the contractile processes in active muscle. The interdependence between the two is undoubtedly intimate, and is readily intelligible on the hypothesis just outlined that alterations of the surface-tension of the contractile elements, conditioned by variations in their electrical surface-polarization, form the immediate condition of contraction. Any hypothesis which fails to explain this interconnection must be regarded as seriously deficient.

I shall now discuss more fully what is usually regarded as the alternative hypothesis, namely, that the contractile energy is due to changes in the surface-tension of certain muscle-elements. In contraction the surface-tension of these elements is supposedly in-

\* Since the electrical potential of the whole cell-interior changes, and with it one of the factors in the conditions of equilibrium of the electrical double layers at the polarized surfaces within the cell.

creased. If this increase of tension is sufficiently great, and the area of the active surface sufficiently large, the transformable surface-energy, which is measured by the product of these two factors, may be sufficient to account for the work done by muscle in contraction. The main question is whether the evidence justifies us in assuming the existence of such conditions in the living muscle-cell. Now the possible range of alteration in the surface-tension of the colloidal contractile elements under the influence of changing electrical polarization is undoubtedly small—almost certainly less than ten dynes per linear centimeter—so that in order to develop the force observed in contraction a very large active surface would be required. Bernstein has shown that any possible alteration of surface-tension at the surface of the muscle-fibrils is quite insufficient to account for the work done by contracting muscle; and he has therefore assumed that in its ultimate structure the fibril is built up out of smaller ellipsoid contractile elements, by the alteration of whose surface-tension the contraction of the whole fibril is produced. By ascribing sufficiently small dimensions to these elements it is possible hypothetically to enlarge the surface to the required degree. But is such an assumption reconcilable with our present knowledge of muscle-structure? In Hürthle's photographs the fibril-segments show a subdivision into narrower rodlet-like structures ("Stäbchen") which he regards as the ultimate contractile elements. The united surface-area even of these elements is also far from sufficient to meet the requirements. There are thus no microscopically demonstrable structures corresponding to Bernstein's hypothetical ellipsoids. It is necessary, if the hypothesis is not to be abandoned, to inquire if still smaller elements may not exist by the alteration of whose surface-tension the requisite mechanical energy may be produced. There is, as I have pointed out elsewhere, good reason to regard the ultimate colloidal particles of the fibrils as corresponding to such elements. By their union to form larger particles, as in the general process of colloid-coagulation, sufficient mechanical energy to account for



contraction might conceivably be freed, since the reduction of surface-area in such a process may be very great, implying a correspondingly large transformation of surface-energy. It is known that in the precipitation of colloids by electrolytes a fundamental condition of the effect is a lessening of the contact-potential of the particles against the medium; the isoelectric point, where the contact-potential is zero, is typically the point of maximum instability, *i. e.*, the tendency to fusion of the particles is then greatest; apparently their surface-energy, then no longer compensated by the electrical energy of the charged surfaces, draws the particles together until a new condition of equilibrium with lessened surface is reached. Increased surface-tension resulting from decrease or disappearance of the surface-charges is in fact now regarded as one of the chief conditions determining the union of the colloidal particles to form larger complexes. This union, if it proceeds sufficiently far, leads to the coagulation or precipitation of the colloid.

Now if in a contractile tissue the mechanical energy appearing in contraction is the expression of a temporary coalescence of the colloidal particles of the fibrils, due to their increased surface-tension, any condition furthering contraction ought, if not rapidly reversed, to lead to further fusion of particles and eventually to visible coagulation. Various facts of comparative physiology show that during conditions of extreme contraction the colloids of contractile tissues do frequently undergo a more or less evident coagulation. The most striking instance known to me is that of the swimming plates of ctenophores; these structures, when immersed in pure isotonic solutions of sodium salts, exhibit for a short time an abnormally accelerated contractile rhythm accompanied by a progressive coagulation of the normally transparent contractile substance; this coagulation is the more rapid and complete the more energetic the contractile movements. Pütter in his recently published "*Vergleichende Physiologie*" cites (p. 456) a number of instances where contraction of muscle is accompanied by a visible coagulation of the muscle-substance. In

vertebrate muscle the coalescence of colloidal particles—assuming it to take place—does not normally lead to visible coagulation during contraction. But it is characteristic of this tissue that the contraction is instantly and automatically reversed unless a rapid and rhythmical process of stimulation is continued. This peculiarity, which is perhaps the most remarkable property of this tissue, is favorable to, or at least quite consistent with, the view that a temporary coalescence of the colloidal particles occurs at each stimulation—due to a depolarization of the surface of the particles, simultaneously with a depolarization of the plasma-membrane of the entire cell—and that this coalescence is instantly reversed by the automatic return of the membrane to its normal polarized condition. If, however, the plasma membrane becomes *permanently* depolarized, as in consequence of any marked and permanent increase in ionic permeability (such as occurs during cytolysis), the coalescence of colloidal particles becomes permanent, and a visible coagulation, typically accompanied by a permanent shortening or "contracture," follows. Such an effect is produced if a frog's muscle is immersed in physiological salt solution containing saponin or other cytolytic substance. If the muscle is first sensitized by exposure for a few minutes to a pure isotonic solution of a sodium salt, such as iodide, the cytolytic action of the saponin is accelerated; the contraction is thus rendered quicker and more energetic and the degree of coagulation is greater; *i. e.*, the energy of the contraction shows a distinct parallelism with the energy of the coagulative process in the muscle-substance. It might be maintained that the coagulative change is merely a secondary consequence of the cytolysis, and has no direct connection with the contraction, but when these facts are taken in conjunction with the others cited in this paragraph the indications seem strong that the ultimate process causing contraction is essentially the same as that which—if carried far enough—leads to coagulation of the colloids. As already pointed out, the latter process is due to fusion of colloidal particles to form larger aggregates; what causes

the union appears to be heightened surface-tension resulting from diminished electrical surface-polarization; the increased tension then draws the particles together and thus performs a certain mechanical work. Similarly in the contractile tissue; within each fibril the colloidal particles or submicrons—which presumably are already in contact or cohere since the whole fibril forms a solid gel-like system—draw together more closely during contraction in consequence of a sudden increase in their surface-tension. This coalescence occurs only within each fibril, not between adjacent fibrils, hence the motion of displacement of the particles is virtually limited to the direction of the long axis and in consequence the whole fibril shortens. As the coalescence of the particles proceeds the active surface-area steadily decreases, and with it the contractile force; hence this force is greatest at the beginning of contraction and diminishes as the muscle shortens.

We assume therefore that in contraction the colloidal particles, especially those of the anisotropic segments, draw together or coalesce. There is, in other words, a clumping or flocking of the particles, which is most rapid and energetic in those regions where the particles are most numerous and closest together. In so doing they displace the more fluid interstitial substance. This incidental displacement of fluid is as necessary an accompaniment of the act of contraction as the coalescence of the particles, and if the contraction is to be rapid and quickly reversible the movement of the fluid must be equally so. It is this consideration, in my belief, which explains the advantage of the segmented structure. The fluid displaced from each anisotropic segment during coalescence of its particles gathers in the adjacent isotropic segments. These appear therefore to increase in volume during contraction (Hürthle), but the apparent transfer of fluid between these regions is merely the visible expression of its displacement from the anisotropic segments by the coalescing particles within the latter. Evidently the quickness and readiness with which the transfer of fluid occurs will increase with the area of the surface separating

the two regions. The disposition of the contractile material of the fibril in numerous small denser segments separated by narrower segments of looser texture (*i. e.*, with wider interstitial spaces) allows for the rapid displacement of the fluid by the colloidal particles as they coalesce; in other words, minimizes the resistance to such coalescence, and is hence a necessary condition for any rapid movement. In the reverse process of relaxation the original relative distribution of the solid and the fluid portions of the system is regained with equal readiness.

Conditions in a colloidal system of this segmented structure are thus highly favorable to rapid and promptly reversible contractile movements due to a massing or flocking of colloidal particles. The striated muscle-cell as a whole need lose no water in contraction; there is merely a temporary redistribution of the more fluid portion of the tissue within the cells. The case of the vertebrate smooth muscle fiber is different, and there is good evidence that in this tissue fluid does actually leave the cell during contraction. The characteristic slowness of both contraction and relaxation in smooth muscle may conceivably be explained on the supposition that the fluid displaced by the contraction of the intracellular fibrillar system can collect only in the relatively large intercellular spaces, *i. e.*, must pass across the plasma membrane, instead of collecting in numerous minute intracellular spaces as in striated muscle. The transfer of fluid is thus necessarily gradual, and the contraction and relaxation are correspondingly slow.

The massing of the colloidal particles in the anisotropic segments results in a shortening and thickening of these segments and hence of the whole tissue. The advantage of having all the segments of the different fibrils within the same cell equal in size and situated at the same level becomes evident on further consideration. In a system of closely crowded contractile fibrils the mechanical processes in contiguous fibrils would clearly interfere with one another were this not the case. The overflow of the displaced fluid into the isotropic segments in any fibril would be impeded, and

the coalescence of the colloidal particles thus checked or prevented, if during contraction the isotropic segments were in close contact with the anisotropic segments of other fibrils; as the latter thickened they would compress the isotropic segments of the fibril under consideration, and prevent the passage of fluid into these latter. Prevention of the displacement of fluid would however retard or prevent the coalescence of the particles, and hence the whole dependent contraction. Such interference between adjacent fibrils would obviously be minimal with a parallel disposition of fibrils, such as we actually find in the tissue. This arrangement is thus mechanically the most advantageous conceivable for a tissue whose effective action depends on the simultaneous contraction of a large number of closely crowded fibrils of the above conceived structure.

We conclude therefore that the physiological advantage of both the segmented structure and the parallel arrangement of the fibrils consists in the provision thus made for a rapid to-and-fro displacement of the fluid part of the fibrils during contractile activity. This displacement of fluid is, however, to be regarded as merely incidental to the contraction, and not as its immediate cause; and in this respect the theory supported above differs fundamentally from those according to which

the transfer of fluid is in itself the essential or "inogenetic" part of the process. It is of course obvious that any theory which (*e. g.*) regards contraction as due to a swelling of the isotropic segments by fluid absorbed from the anisotropic—as discs of gelatin or fibrin swell in acidulated water—must require that the interchange of fluid should be rapid and promptly reversible; hence that part of the present interpretation which regards the structure of striated muscle as essentially a means for facilitating transfer of fluid within the fibrils is equally consistent with this latter theory. Nevertheless the point of view that regards absorption of water by an acidulated sheet of gelatin as the analogue of what occurs in muscular contraction is radically different from that set forth in this paper, according to which the energy of contraction is the transformed surface-energy of the ultimate structural elements or colloidal particles (sub-microns) composing the fibrils. There is undoubtedly a movement of fluid between the muscle-segments during contraction; but this fact in itself is consistent with either of the two theories just contrasted. The decision between the two must be made on the basis of other evidence.

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## COMPLETE DISCHARGE OF MITOCHONDRIA FROM THE SPERMATOZOON OF PERIPATUS.<sup>1</sup>

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The following account presents the unique case of a spermatozoon that loses all its mitochondria with the abstriction of the cytoplasm.

In my paper ('00) on the spermatogenesis of *Peripatus balfouri* the history of the germinal cycle was described from the spermatogonia through the maturation divisions, and that is now completed by a description of the spermiogenesis. In that account certain distinctive bodies were figured and discussed under the name of "yolk spherules." These were noted to occur only sparsely in the spermatogonia, but to become abundant during the growth period of the spermatocytes, and in all mitoses to lie outside of the spindles. Similar bodies were seen in the sheath cells of the testis, and I concluded these to be nurse cells, elaborators of the supposed yolk spherules, and that the spermatogonia received their "yolk spherules" from these nurse cells. At the time when that paper was sent to press Benda had not yet published his term mitochondria, and in conformity with the results of other investigators of that day I supposed true yolk to be formed within spermatocytes.

Now I am able to demonstrate that the bodies in question are not yolk spherules, rather chemically quite different from these, but are mitochondria according to their behavior and staining reactions. Indeed, it will probably be found that most bodies described as yolk spherules in spermatocytes are really mitochondria. My early account was therefore one of the first to describe mitochondria through successive cell generations of spermatogenesis. But that account was wrong in its inference that those of the germ cells proper are derived from those of the nurse cells; on the contrary, they occur independently in the

<sup>1</sup>*Note by the Editor.* Professor Montgomery died while this paper was in press. He had therefore no opportunity to make any changes in the proof, and the paper is printed exactly as the manuscript left his hands.

two classes of cells, just as they do in the Sertoli cells and spermatocytes of mammals.

The material consisted of testes, seminal vesicles, vasa deferentia, and oviducts, some fixed in strong Flemming's fluid diluted with an equal part of distilled water, and others preserved in corrosive sublimate-acetic; all were originally received from my friend, Dr. Purcell, of Cape Town. The mitochondria appear pale red after Hermann's safranin-gentian violet, and after the Ehrlich-Biondi-Heidenhain method; shades of gray or black after iron hæmatoxylin, according to degree of destaining; and after Benda's stain they are deep violet, while the chromatin is brownish and the centriole red—the typical reaction to this stain. There is only one other object known to me on which they are equally readily demonstrated, namely, the spermatocytes of *Ascaris*.

Fig. 1, Pl. I., exhibits the position of the mitochondria at the end of the second maturation mitosis where, as after the first also, they lie at the distal poles (equatorial ends) of the daughter cells. Until their later fusion takes place they are chiefly peripheral, next the cell wall, spherical or slightly elongate, and in the form of hollow vesicles. In the earliest spermatids they always form a layer at the distal pole, but sooner or later move forward, along the cell membrane, so as to take a position on the side of the nucleus (Figs. 2-16); at the same time the sphere (*s*) always advances from its original position and the cytoplasm comes to make a lobe around the nucleus and entirely in front of the centriole (*c*). These movements do not occur synchronously on cells of the same stage, there is much variation in the process, yet the end result is the same in all. By reason of the mitochondria remaining generally in a single layer they may be readily counted, and their number is found to differ in different spermatids, which shows their mass cannot be accurately quartered by the maturation divisions. In Figs. 4, 6, 11-13, all of each cell are drawn with care, and their numbers here are respectively: 33, 45, 68, 64, 49. Their volumes also differ considerably, as the figures show. They do not blacken with osmic acid.

In the nucleus the chromosomes are at first peripheral and quite distinguishable (Fig. 2), then coalesce to produce a hollow

chromatin sphere enclosing clear karyolymph (Fig. 3). Next the nucleus lengthens, and distally its chromatin border becomes very thin (Figs. 4, 5, 7, 8); but it could not be determined that at this thin region nuclear sap passes out of the nucleus in the way I have described (1911) for *Euschistus*. This thin area of the nuclear wall later becomes as thick as the remainder (Figs. 9, 10). Then the proximal end of the nucleus becomes pointed (Fig. 10). With its later great elongation (Figs. 11-17, and Plate II.) the nucleus changes its appearance, due apparently to its interior becoming more chromatic, so that on surface views it appears nearly homogeneous throughout; it continues the same affinity for basic stains, and from the stage of Fig. 11 onwards I have drawn it brown and not deep black simply in order to represent the mitochondria more distinctly. Yet cross sections show that even in the mature sperm the chromatin makes a hollow cylinder and not a solid rod.

Now to return to the mitochondria, to describe their particularly notable phenomenon. After all of them have moved forward from the distal pole, carried probably by currents in the lobe of cytoplasm, they fuse together to produce a true Nebenkern or chondriosome (Meves, '00). Figs. 11-16 show them becoming agglomerated, and in Fig. 17 they are seen to be fusing to produce compound vesicles. Fig. 18, Pl. II., exhibits them on the side of the nucleus, with fusion far advanced, and Fig. 19, their consolidation into a chondriosome. As the process of fusion advances they stain more deeply, so that the chondriosomes when completed appear densely chromatic (Figs. 20-22). Sometimes a few mitochondria remain isolated without joining with the others, sometimes all fuse together (Figs. 18-21). Simultaneously the cytoplasmic lobe moves forward along the nucleus, or, probably more correctly, the nucleus moves backward through it; and in its substance appear denser strands and minute granules (Figs. 18, 19) which may be degeneration products comparable with the "tingible granules" of mammals. Consequently, each nearly mature sperm of the seminal vesicle (Figs. 20, 21), as all of the vas deferens (Fig. 22), carries near the anterior end of the nucleus a cytoplasmic lobe with a densely staining chondriosome; there appears to be no cytoplasm at all



in the region of the centriole and the flagellum. Were the history of the spermatozoa unknown beyond their conditions in the vasa deferentia, there would be no evidence of the fate of the cytoplasmic lobes and chondriosomes. But fortunately I have numerous preparations of oviducts from female individuals, all crowded with spermatozoa, and in these all the spermatozoa lack entirely the cytoplasmic lobes and chondriosomes (Figs. 23, 24); in not a single case was a cytoplasmic lobe observed upon a spermatozoön when within an oviduct.

*Peripatus*, accordingly, has for us more than a phylogenetic interest, it has a high cytological importance. The spermatozoön during its development casts off its cytoplasm, and evidently all of it. But this abstriction of the cytoplasm, or a portion of it, is now known to be a quite general phenomenon in animals, and only amphibians and certain insects appear to furnish exceptions to it. Much more important is that all the mitochondrial substance, in the form of a compact chondriosome, is cast away with it. Further, I had previously described the spermatozoön as possessing a lance or perforatorium, staining differently from the nucleus. Now I can demonstrate that this supposed perforatorium stains differently only on account of its excessive tenuity, that it is only the narrowed proximal end of the nucleus, and that it has no connection with the sphere. We have seen that the sphere arises just behind the nucleus (Figs. 2, 3), and moves forward into the cytoplasmic lobe (Figs. 5, 7, 8, 10, 12, 14, 16-19). When the chondriosome is fully developed the sphere lies still in the cytoplasmic lobe, separated from the nucleus (Fig. 20), and no evidence was observed that it moves along the latter to constitute a perforatorium. Therefore it is certain that the sphere as well as the chondriosome becomes thrown off with the cytoplasm.

The history of the centriole was not followed in detail. In the telophase of the secondary spermatocytes a minute centriole is present at each pole (Fig. 1). At the next stage when it was noticed (Fig. 3) it appeared as a much more voluminous body at the distal pole of the nucleus, and it retains this position thereafter. Later it becomes discoidal with indication of subdivision into two parts (Figs. 4-10), and afterwards lengthened in the axis

of the spermatid (Figs. 11-19), reaching its maximum size at the stage of Figs. 13, 14. In the mature and nearly mature spermatozoa it makes a slender rod, joining nucleus and flagellum, and then is seen to have decreased in volume (Figs. 21-24). The flagellum connected with it is a delicate, flattened thread, evidently without spiral membrane or cytoplasmic sheath; in the figures only its proximal portion is shown. In some cases there appeared to be a spiral skeleton around the nucleus, such as Koltzoff (1908) has recently described in other species; but examination proved that in *Peripatus* this is occasioned simply by chance wrapping of a flagellum around the nucleus.

In the mature egg and in cleavage stages no structures were found in any way resembling the mitochondria of the sperm cells.

Meves (1908, and later papers) draws the conclusion that mitochondria are important hereditary elements, directing cytoplasmic activities as the chromosomes direct those of the nucleus, self-perpetuating bodies differentiating during ontogeny into most of the fibrillar structures of the body. Without entering into the rapidly growing literature now, we will be content with the statement that a considerable number of investigators corroborate these views, and that they have been especially elaborated by Giglio-Tos and Granata ('08). This hypothesis more than any other has directed attention to these bodies. Yet they are far less conservative and regular than the chromosomes in number, form and behavior and there is evidence that occasionally some of them are eliminated during spermiogenesis. Thus Fauré-Fremiet has distinguished four types of them: (1) Those that undergo changes of position without profound morphological changes, as in mammalian spermiogenesis. (2) Those that at the same time undergo great structural changes, as in insect spermatids. (3) Those of which only a part change into the chondriosome or Nebenkern of the spermatid, while others degenerate, as in spermatogenesis of certain gastropods. And (4) those that transform wholly or partly into deutoplasmic bodies, some cases of oögenesis. The fourth of these classes cannot be said to be definitely established, but there can be little doubt about the evidence for the third. Thus, besides the instance in gastropod spermatogenesis studied by Fauré-

Fremiet, Retzius noted in mammals a "considerable reduction in their substance as they enter into the formation of the spiral thread." Jordan ('11) found that in spermatids of the opossum a considerable number of mitochondria are cast off with the cytoplasm; and while Duesberg ('10) maintains that in the guinea pig all take part in forming the spiral thread of the spermatozoön, yet he figures granules with similar staining reactions in the dehiscent cytoplasmic lobe. The parallel does not seem yet to have been made, yet may not the "tingible corpuscles" of mammalian spermatids be metamorphosed mitochondria, ones that have nothing to do with the spiral threads? And now we are able to adduce the positive case of *Peripatus*, in which all the mitochondria become removed from the spermatozoön.

In view of these facts it seems to me we should be very cautious in attributing to the mitochondria a rôle in cellular activity at all equal to that of the chromosomes. No spermatozoön ever discards chromosomes, but that of *Peripatus* throws off all its mitochondria.

## LITERATURE CITED.

**Duesberg.**

- '10 Nouvelles recherches sur l'appareil mitochondrial des cellules séminales.  
Arch. Zellf., 6.

**Fauré-Fremiet.**

- '10 Étude sur les mitochondries des Protozoaires et des cellules sexuelles  
Arch. Anat. Micr., 11.

**Giglio-Tos e Granata.**

- '08 J mitocondri nelle cellule seminali maschili di *Pamphagus marmoratus*  
(Burm.). Biologica, 2.

**Jordan.**

- '11 The Spermatogenesis of the Opossum, etc. Arch. Zellf., 7.

**Mees.**

- '00 Ueber den von v. la Valette St. George entdeckten Nebenkern (Mitochondrienkörper) der Samenzellen. Arch. mikr. Anat., 56.  
'08 Die Chondriosomen als Träger erblicher Anlagen. Ibid., 72.

**Montgomery.**

- '00 The Spermatogenesis of *Peripatus balfouri* up to the Formation of the Spermatid. Zool. Jahrb., 14.

**Montgomery.**

- '11 The Spermatogenesis of an Hemipteron, *Euschistus*. Journ. Morph. 22.

## EXPLANATION OF PLATES.

All figures were drawn with the cameral lucida at the level of the base of the microscope, Figs. 13, 20 with Zeiss apochr. 1.5 mm., oc. XII., the others with Zeiss achr. 1/12 mm., oc. XII. Figs. 1-3, 5, 7-12, 14-19 from a seminal vesicle, Flemming's fluid, iron hæmatoxylin; Figs. 4, 6, 21 from a seminal vesicle, corrosive sublimate-acetic, iron hæmatoxylin; Figs. 13, 20 from a seminal vesicle, Flemming's fluid, Benda's stain; Fig. 22, from a vas deferens, Flemming's fluid, safranin-gentian violet; Fig. 23, from an oviduct, treated like the last; Fig. 24, from an oviduct, corrosive sublimate-acetic, iron hæmatoxylin.

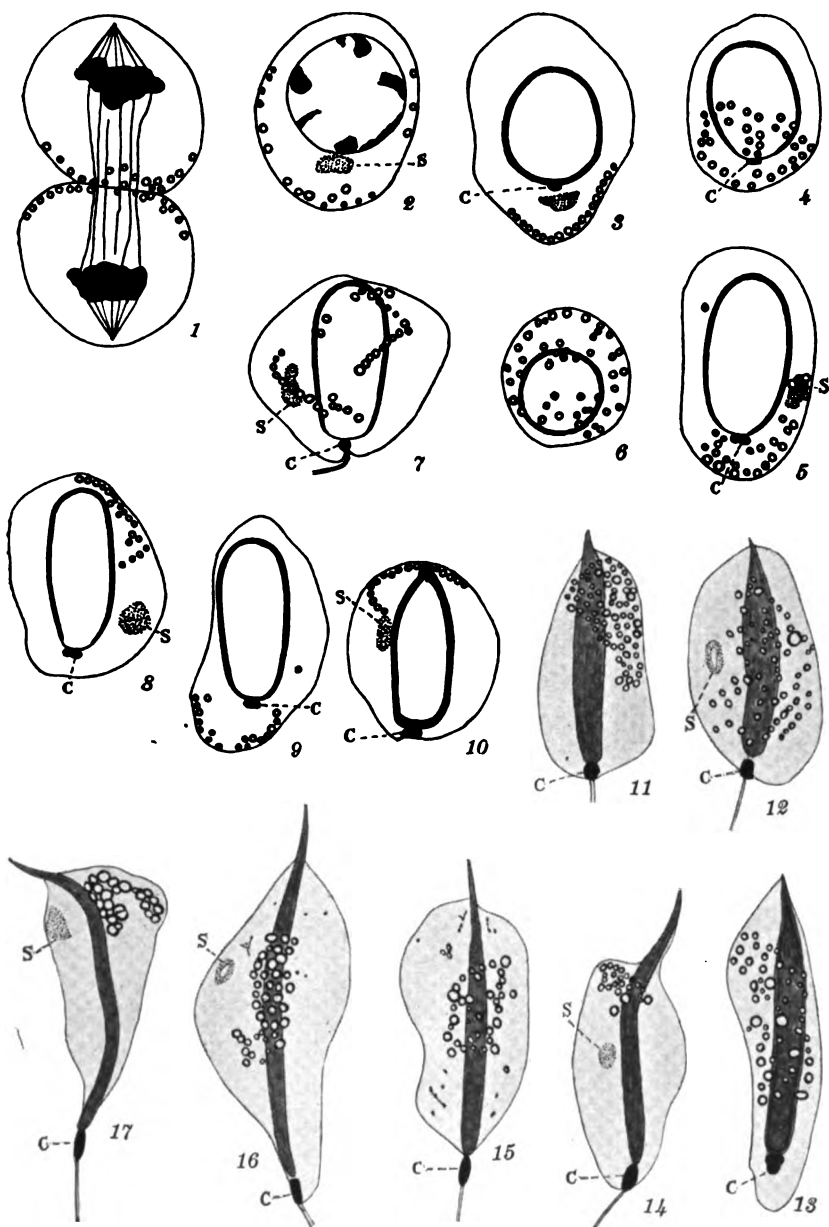
*c.*, centriole.

*s.*, sphere.

## PLATE I.

FIG. 1. Telophase of second maturation mitosis.

FIGS. 2-17. Successive stages of spermiogenesis from the seminal vesicle. Fig. 6 is an apical view of the stage of Fig. 5.



T. H. MONTGOMERY.





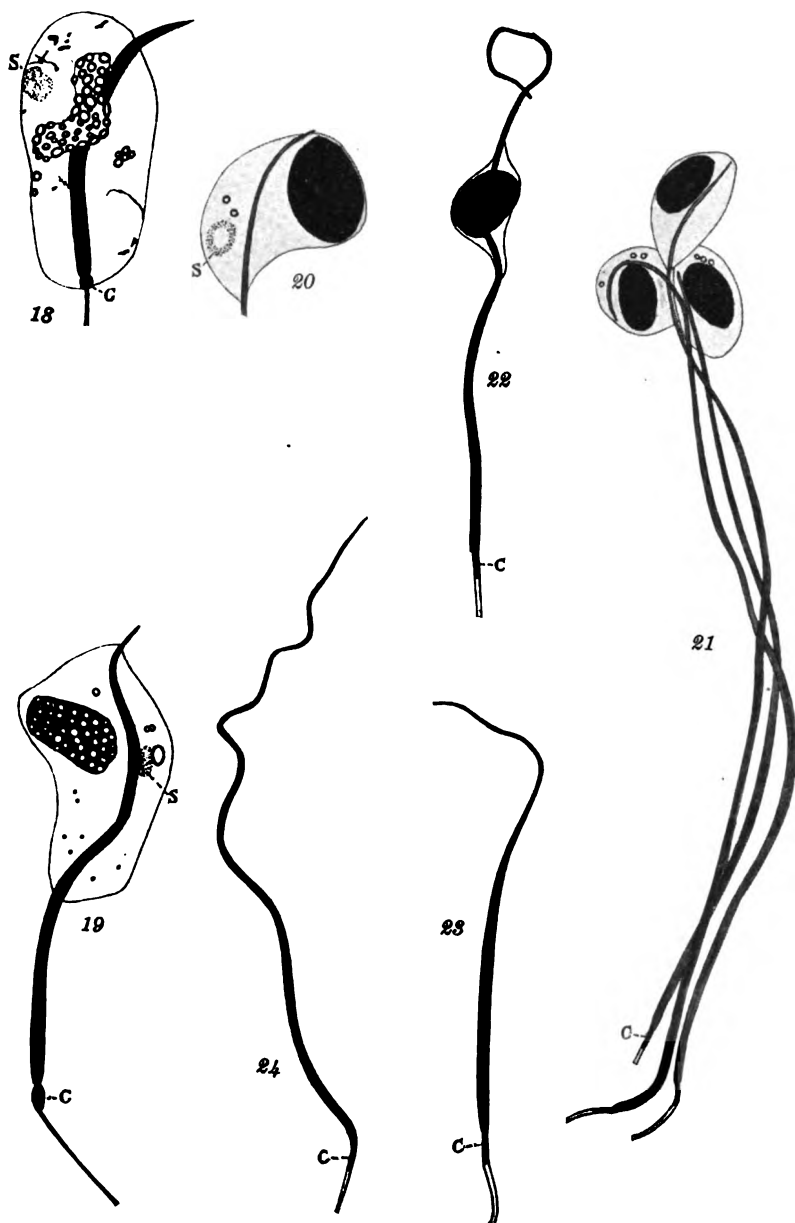


## PLATE II.

FIGS. 18-21. Later stages of spermiogenesis from seminal vesicle. In Fig. 20 only the cytoplasmic lobe and the proximal portion of the head are shown.

FIG. 22. Spermatozoön from vas deferens.

FIGS. 23, 24. Spermatozoa from oviduct.



T. H. MONTGOMERY.



**THE LEECHES OF MINNESOTA**  
**PART III**

**CLASSIFICATION OF THE LEECHES OF MINNESOTA**

**BY**

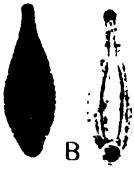
**J. PERCY MOORE**







A



B



D



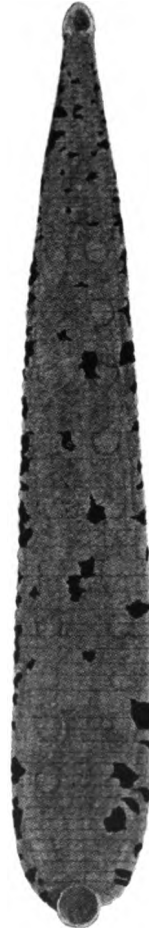
F



C



G



G



A-Glossiphonia stagnalis  
B-Glossiphonia complanata  
C-Macrobodella decora

G-Haemopsis marmoratis

D-Placobdella parasitica  
E-Haemopsis grandis  
F-Erpbodella punctata

## INTRODUCTION

That the lake region of Wisconsin, Minnesota and Manitoba abounds in leeches of large size and great variety has long been known, and has been commented upon frequently by visitors to that well-watered area. The very first recognizable descriptions of North American leeches, published by Thomas Say in 1824, were based upon examples observed in the territory about Lake Vermillion in Minnesota. Since that time a number of additional species have been described from localities about the western end of Lake Superior.

The richness of the leech fauna of Minnesota is fully established by the splendid collections, gathered by the State Zoological Survey under the direction of Professor Henry F. Nachtrieb, which form the chief basis of this report. The entire State is not represented in the collection, most of which came from the northern section, chiefly from Lake Vermillion, Leech Lake, Mille Lacs and their environs. Yet it includes twenty species—a number probably greater than could be found in an area of equal size elsewhere in the United States, or, so far as has been recorded, anywhere else in fresh water. Leeches generally have a wide geographical distribution and the presence of most of these species in other parts of the state is to be expected, as many of them range through the entire northern tier of states or even beyond, several are circumpolar, and one, *Glossiphonia stagnalis*, is almost cosmopolitan. The occurrence of a considerable number of the species in the southern portion of Minnesota has been ascertained through material received from other sources, the most important being a collection sent to me by Prof. Henry L. Osborn, which, indeed, adds one species, *Placobdella hollensis*, not represented in the Survey collections.

The plan of this report is to give descriptions, which are something of a compromise between the technical and popular, of the salient features of the entire organization of each species, omitting altogether those minutiae which require more than a simple microscope or ordinary methods of dissection for their verification. Fuller descriptions of many of the species will be found in a paper by Castle, Some North American Fresh-water Rhynchobdellidae,



in the Bulletin of the Museum of Comparative Zoology, Vol. XXXVI, (1900) pp. 16 to 64, and one by Moore, The Hirudinea of Illinois, in the Bulletin of the Illinois State Laboratory of Natural History, Vol. V (1901) pp. 479-547. The literature lists included in these two papers will enable one to ascertain the principal papers in which North American Hirudinea have been discussed.

Characteristic features in the anatomy or exterior have been figured for all of the species, in most cases from Minnesota representatives, but new species or those which have not been figured previously are treated in greater detail.

Of the biological relations of leeches to other animals much remains to be learned and this field affords a rich opportunity for exact observation. Likewise the breeding and other habits of many species are unknown or known only imperfectly. The remarks on this side of the subject which follow the descriptions are based on observations made chiefly in the vicinity of Philadelphia.

The drawings of the frontispiece are colored from living examples taken, with the exception of *Hæmopsis grandis*, near Philadelphia.

**KEY TO THE SPECIES  
OF  
MINNESOTA LEECHES**



## KEY TO THE SPECIES DESCRIBED IN THIS PAPER

The bold-faced numbers refer to the page.

I. Mouth a small pore-like opening in the disk of the anterior sucker, through which a muscular pharyngeal proboscis may be protruded.

A. Complete somites formed of three annuli.

a. Genital orifices separated by a single annulus; eyes one pair, distinct.

b. A dark brown cuticular plate and underlying gland on the dorsum of somite VIII.

1. Body capable of great extension; color pale—pink, gray or brownish.

**Glossiphonia stagnalis, 77**

bb. No nuchal plate or gland in the adult.

2. Body very slender, elongated and little flattened; very transparent owing to the nearly complete absence of pigment; no cutaneous papillae.

**Glossiphonia nepheloidea, 76**

3. Body relatively broad and flat; more or less heavily pigmented with brown arranged in linear pattern, annulus *a2* marked by white spots usually arranged in transverse rows; three longitudinal series of conspicuous black papillae.

**Glossiphonia fusca, 80**

aa. Genital orifices separated by two annuli; eyes in several pairs.

4. Three pairs of eyes; gastric cæca six or seven pairs; a pair of dark longitudinal lines both above and below.

**Glossiphonia complanata, 82**

5. Four pairs of sub-equal eyes, all simple; gastric cæca nine pairs. **Hemiclepsis occidentalis, 96**

6. One pair of compound eyes followed by three or more pairs of much smaller simple eyes; gastric cæca seven pairs.

**Plocabdello hollensis, 94**

- aaa. Genital orifices separated by two annuli; a single pair of compound eyes; gastric cæca, seven pairs, branched.
- b. Somites I to V much widened to form a distinct head.
  - 7. Somites I and II biannulate; the dorsum marked by three strong papillated keels; gastric cæca much branched. **Placobdella montifera, 88**
- bb. Anterior somites not especially widened.
  - c. Posterior sucker very free and supported on a slender peduncle; anus at XXIII/XXIV; gastric cæca little branched.
  - 8. Body rather high, very contractile; dorsal papillae wanting. **Placobdella pediculata, 90**
  - cc. Posterior sucker not supported on a specially slender peduncle; anus at XXVII/XXVIII; gastric cæca much branched.
  - 9. Body very much depressed; dorsal papillæ few, low and smooth; integuments rather opaque. **Placobdella parasitica, 84**
  - 10. Body very much depressed; dorsal papillæ numerous, rough and usually high; integuments translucent. **Placobdella rugosa, 86**
- AA. Complete somites composed of more than three annuli.
  - 11. Complete somites consisting of six unequal annuli; posterior sucker very large and provided with a marginal circle of contractile papillæ; eyes one pair contiguous in middle line. **Actinobdella inequiannulata, 99**
  - 12. Complete somites consisting of twelve or fourteen approximately equal annuli; body divided into two regions; posterior sucker without marginal papillæ; eyes widely separated on posterior part of head. **Piscicola punctata, 103**
- II. Mouth large, the sucker appearing as its bounding lips; the pharynx not forming a protrusible proboscis.
  - A. Eyes five pairs, arranged in a regular arch on somites II to VI; genital ducts with complex copulatory apparatus; testes strictly paired, their number moderate; at least one pair of gastric cæca present.

- a. Jaws prominent, bearing many small teeth arranged in one series; accessory copulatory glands present and opening in pores behind the female genital orifice.

13. Teeth about sixty-five in each jaw; genital pores separated by five annuli; the dorsum marked with median red and marginal black spots, both metameric.

***Macrobdella decora*, 106**

- aa. Jaws prominent, bearing a few coarse teeth arranged in paired series; no accessory copulatory glands.

14. Teeth twelve to sixteen pairs on each jaw; the primary annuli VIIa<sub>3</sub> and VIIIa<sub>1</sub> enlarged, but only partially divided into secondary annuli; color variable but marked more or less thickly with non-metameric black blotches.

***Hæmopsis marmoratis*, 110**

15. Teeth twenty to twenty-five on each jaw; the secondary annuli VIIb<sub>5</sub> and b<sub>6</sub> and VIIIb<sub>1</sub> and b<sub>2</sub> completely formed; color nearly uniform, usually with a median dorsal dark stripe and few or no blotches.

***Hæmopsis lateralis*, 113**

- aaa. Jaws absent or rudimentary; no teeth; no accessory copulatory glands.

16. Male genital orifice at XI b<sub>5</sub>/b<sub>6</sub>; the female at XIIb<sub>5</sub>/b<sub>6</sub>; color pattern consisting in part of close or distant blotches of dark pigment, ventral ground color lighter than dorsal.

***Hæmopsis grandis*, 117**

17. Male and female genital orifices constantly at the middle of XIb<sub>6</sub> and XII b<sub>6</sub> respectively; a few distant dorsal blotches or none; no ventral blotches, ventral ground color not paler, usually darker than dorsal, the rufous or orange marginal stripe conspicuous.

***Hæmopsis plumbeus*, 115**

- AA. Eyes three or four pairs, not arranged in a regular arch, two pairs situated on somite IV; genital ducts relatively simple, without complex copulatory apparatus; testes numerous, not regularly paired; no gastric cæca.

- a. Annulus *b6* not obviously enlarged and subdivided.  
18. Eyes three pairs; male orifice at XII*b2/a2*, female at XII*b5/b6*; atrial horns simply curved and vas deferens reaching forward to the level of ganglion XI.

***Erpobdella punctata*, 121**

- aa. Annulus *b6* obviously enlarged and subdivided.  
19. Eyes four pairs; male orifices at XII*b2/a2*, female at XII *b5/b6*; atrial horns spirally turned, vas deferens reaching forward to the level of ganglion XI.

***Nephelopsis obscura*, 123**

20. Eyes four pairs; male orifice at XII *b1/a2* or occasionally XII *a2/b5*, the female at XIII *b1/b2*, atrial horns simply curved, vas deferens reaching forward to ganglion XI.

***Dina parva*, 125**

21. Eyes three or four pairs; male orifice at XII *b2/a2*, female at XII *b5/b6*; atrial horns simply curved, vas deferens not reaching anterior to atrium. ***Dina fervida*, 127**

**DESCRIPTIONS**  
**OF**  
**FAMILIES, GENERA AND SPECIES**





## DESCRIPTIONS OF FAMILIES, GENERA AND SPECIES

### Family Glossiphonidæ.

Leeches of medium or small size; generally rather short, broad and much flattened, rarely slender and elongated. No distinct clitellum. Caudal sucker usually large and flat; oral sucker rather small and, except in a few cases, scarcely expanded. Complete somites of middle region usually of three rings, rarely of 2, 5 or 6. Eyes 1-4 pairs, situated in a longitudinal row close to the median line; the first pair often compound, the others simple. Dorsum often studded with cutaneous papillae in addition to metameric sensillae. Mouth a small pore in the oral sucker. Pharynx a slender, protrusible proboscis without jaws or teeth. Salivary glands present. Stomach with from one to ten pairs of lateral, simple or branched cæca. Intestine with four pairs of cæca. Genital orifices separated by one to four rings, the ♀ in somite XII and the ♂ in XII or between XI and XII. Testes sacs usually six, rarely nine pairs; sperm ducts divided into a very slender vas deferens and a large epididimis and ductus ejaculatorius, the latter of which opens into a small median atrium without a penis. Ovisacs a pair of slender convoluted tubules opening together at the female orifice without a vagina. Fertilization by means of horny spermatophores attaches to the integument from which the spermatozoa penetrate the tissues to the ovisacs. Eggs and young borne on the ventral surface of the parent. Strictly fresh water. Tortoise and snail leeches, which feed on snails, small worms, etc. or suck the blood of tortoises, frogs or fishes, rarely fixed parasites of the latter. Creepers, mostly poor swimmers.

### Genus *Glossiphonia* Johnston.

Moderately depressed or elongated and nearly terete. Eyes 1-3 pairs, all simple. Cutaneous papillae few or none, never strictly median. Pharyngeal salivary glands diffuse; gastric cæca 1-7 pairs, simple or slightly branched. Sperm ducts forming a pair of long, open loops extending through several segments. Chiefly free-living or attached to invertebrates.

**Glossiphonia nepheloidea (Graf).**

(Plate I, fig. 2)

*Clepsine nepheloidea* Graf (1899).*Glossiphonia elongata* Castle (1900).

Description—This species, which may be called the worm leech, is readily distinguished from any other member of its family belonging to this fauna by its slender, elongate, and sub-terete form. Slightly smaller and much narrower than *G. stagnalis* its great power of extension permits full grown individuals to exceed that species in length. Both the head and caudal sucker are very small and weak, and the axis of the latter nearly coincides with the axis of the body. A single pair of widely separated eyes show their faintly pigmented cups within the anterior part of somite IV. The skin is smooth and lacks integumental papillæ altogether; the muchal gland and plate are also lacking in the adult.

For the most part the annuli are very distinct, regular, smoothly rounded and simple, but the furrows of the head region are mostly faint and usually require special preparation to make them visible. Somites I and II are united into a single annulus or are separated only by a faint furrow; III, IV, and V are biannulate, the first annulus being the larger in each case; VI to XXIV, inclusive, are triannulate, and XXV, XXVI and XXVII each uniannulate but distinct.

The relatively large mouth is located in somite III. In correlation with the narrowness of the body the stomach is a nearly simple straight tube bearing the last pair of reflexed cæca only, and even these are shorter than in allied species. The salivary glands are small and of the diffuse type.

As is the condition in many of the smaller species of *Glossiphonia* the genital orifices are separated by only one annulus, the male being in the furrow XII  $a_1/a_2$ , the female XII  $a_2/a_3$ . There are six pairs of testes occupying the customary positions, and the vas deferens is folded into a long post-atrial loop, the terminal limb of which is an enlarged sperm sac. The longitudinal musculature is weak and diffuse.

The body of the species, particularly in its anterior part, is remarkable for its transparency and is almost totally devoid of superficial pigment. The walls of the stomach and intestine exhibit more or less of a yellow or pale orange color which is the prevailing tint of the posterior region of the body.

Habits—*Glossiphonia nepheloidea* is by no means an abundant leech and has been until recently generally overlooked, a result no doubt in large part due to its inconspicuous coloring and seclusive habits rather than its scarcity. Only four specimens, all taken from Lake Pepin by means of a pump, represent the species in the Minnesota collections. Whitman, Graf and Castle have found it only in ponds in Massachusetts. In my experiences it occurs much more numerous in running water among plants, particularly along the muddy flats exposed at low water along the Delaware River, associating with *G. stagnalis*, *G. complanata* and sometimes other species.

In appearance and movements it is much more worm-like than any other species of *Glossiphonia*. Its weak suckers and deficient musculature ill fit it for active creeping and, being incapable of swimming and of a manifestly sluggish disposition, it moves about but little and chiefly in the very unleechlike manner of crawling through the ooze. When exposed in its place of concealment it writhes and twists in a peculiarly helpless fashion, often for a long time not even attempting to attach the suckers and never exhibiting that decision of movement and promptitude to seek concealment which is shown by *G. stagnalis*. Its means of protection consist largely in the very copious mucous secretion which envelopes the body when irritated.

Although, like *G. stagnalis*, this leech will feed on snails and worms and even suck blood when the opportunity offers, it is essentially a scavenger and feeds largely on the substance of dead animals and on ooze.

***Glossiphonia stagnalis* (Linn.) Johnston.**

(Plate I. fig. 1.)

*Hirudo bioculata* Bergmann (1757)

*Hirudo stagnalis* Linnaeus (1758)

*Clepsine modesta* Verrill (1872)

*Helobdella stagnalis* Blanchard (1896)

Description—*Glossiphonia stagnalis* is a small leech somewhat larger and decidedly stouter than *G. nepheloidea*. Large individuals may reach a length of an inch when fully extended and in that state would be fully twice the width of a *G. nepheloidea* of the same length. When contracted to one-half that length, which is about the ordinary resting condition, they would be about three

times the width of *G. nepheloidea* and much more flattened, but still decidedly convex above. The head is small but moderately distinct, less elongated and more strongly annulated than in *G. nepheloidea*. The caudal sucker is well developed, strongly directed ventrad, and but little exposed posteriorly; its axis ordinarily at about right angles to the body axis. While only one pair, situated as in *G. nepheloidea*, the eyes are much more conspicuous owing to the greater amount of their pigment. A conspicuous feature is the more or less deep brown chitinous plate and underlying gland situated on the dorsum of VIII *a1* and *a2*.

There are no distinct integumental papillae though the surface may be somewhat roughened with scattered sense organs. The metameric sensillae are inconspicuous as in *G. nepheloidea*.

The annulation is distinct throughout, especially at the caudal end, where the annuli are angulated at the margins. Somites I and II are usually completely united in the short prostomium; III is uniannulate or occasionally faintly subdivided; IV and V are biannulate, the latter more completely and sometimes showing indications on the dorsum of the furrow *a1/a2*; VI to XXIV are triannulate, and XXV and XXVI biannulate, the latter occasionally being united with XXVII, which is commonly represented by a pair of wedged-shaped halves nearly sundered by the anus.

The mouth is smaller but otherwise similar in form and position to that of *G. nepheloidea*. Diffuse salivary glands extend through somites XII to XIV or sometimes farther. Never more than six pairs of gastric cæca are present, but the number is variable and may be reduced to three pairs by the obliteration of the first three. All are simple and unbranched and increase in size from the first to the sixth pair, the last being much the largest and reflexed caudad through three or four somites (XIX to XXII).

The external genital orifices and the reproductive organs generally are essentially like those of *G. nepheloidea*. The longitudinal muscle cells are arranged diffusely but are strongly developed.

Pale gray, pink, brownish or greenish tints, which are much affected by the contents of the alimentary canal seen through the more or less translucent tissues, are the colors of this species. Young specimens and some adults are almost colorless and translucent, but commonly the tissues of the larger ones are rendered opaque by the presence of numerous reserve and pigment cells.

Habits—Judging by the material which represents it in this collection this nearly cosmopolitan species must be much less abundant in the lakes of Minnesota than in many other sections of this country and especially the northeastern portion from Illinois to Maine. It is found everywhere but abounds especially in warm shallow waters of streams, pools and ponds and along the shores of lakes and rivers; it is the common pond leech. In all suitable localities it gathers in numbers on the under sides of stones, sticks and fallen leaves or conceals itself between the ensheathing leaf stalks of rushes and other aquatic plants. Less often it attaches itself to the bodies of larger leeches, such as *Macrobdella* and *Haemopsis*, to fresh water snails, mussels, fishes, turtles and more rarely to frogs. It is perhaps transported on the legs of aquatic birds. Like most of the *Glossiphoniæ* it does not swim, but when disturbed creeps with considerable activity to a place of concealment, when, if still further disturbed, it rolls into a ball in the manner of a "pill bug" and falls to the bottom, then quickly unrolls and creeps away to a dark shelter.

Ordinarily its food consists of small annelids, insect larvæ, snails, and small bivalves like *Pisidium* and its allies. Numbers also congregate and feed upon dead bodies of larger animals, such as crustaceans, fishes and frogs; and when occasion offers blood will be drawn from injured fishes, frogs and other vertebrates, including the feet of wading boys. Vast numbers frequent the fishing stations along the Delaware River, attracted no doubt by the quantities of bloody offal thrown into the water at such places. Under such conditions the stomach of every individual will be distended with blood, and, comparing Castle's description of the alimentary canal with my own observations, I am led to suspect that the capacity of the gastric cæca may be increased in individuals which habitually subsist upon such diet.

On the other hand this little leech is frequently devoured by the large predaceous leeches, sunfish, perch and other small carnivorous fishes. Along the shores of tidal rivers, like the Delaware, various species of snipe and sandpipers, which feed on the flats exposed at low water, pick them from the shingle and gravel.

Breeding begins in early spring and extends into the early summer. During the latter part of April and early May almost every individual bears its burden of eggs or young. In streams and ponds of cold water ovi-position occurs later than in warmer waters. In

some localities a second brood is raised in late summer. As in most closely related forms the eggs are not attached directly to the body but are contained several together in small mucoïd sacs, of which mature individuals bear from eight to twelve or fifteen attached to the posterior ventral surface. When bearing eggs or young the rhythmic oscillating respiratory movements become much more frequent and vigorous than at other times. When disturbed the brood is protected by enveloping it in the margins of the body folded toward the middle line and by rolling into a ball.

**Glossiphonia fusca** Castle.

(Plate I, fig. 3)

*Clepsine papillifera* var. *lineata* Verr. (1874)

not *Hirudo lineata* Müller (1774)

*Glossiphonia lineata* Moore (1898)

*Glossiphonia fusca* Castle (1900)

Description—The form is rather short and thick and relatively broader than the other small *Glossiphoniæ* described in this paper. In size it is about equal to *G. stagnalis* but lacks the great power of extension of that species. Typically the back bears three longitudinal series of small but prominent sharp conical papillæ, an irregular median series, really formed of a pair of closely approximated series reduced to one by fusion or loss of some of the members, and two dorso-lateral series situated half-way between the middle and the margins. Sometimes two more are added external to the latter, one on each side, but these latter are always very incomplete. There is a single pair of remarkably large eyes situated as in *G. stagnalis*. No nuchal gland is present.

Somites I and II are uniannulate or completely united; III and IV are biannulate, the larger annulus of the latter partly divided by an incomplete furrow  $a_1/a_2$ ; V is generally triannulate dorsally, but biannulate ventrally. Somites VI to XXIV are fully triannulate, XXV and XXVI biannulate, the latter incompletely in most cases, and XXVII uniannulate. The postanal annulus is very large.

The mouth is situated as in *G. stagnalis* but is rather larger and the proboscis wider than in that species. There are six pairs of gastric cæca, strictly simple or slightly lobed, and the first is sometimes wanting; the last reflexed as usual. The salivary glands are diffuse but much more extensively developed than in the preceding species.

The testes are present in the same number and occupy the same positions as usual, each lying just anterior to the base of one of the gastric cæca. A long posterior loop of the vas deferens, partly enlarged as a sperm sac, is developed and extends through the ventral sinus to somite XV or beyond.

The colors are plain but very pretty and exhibit a considerable range of variation. The ground is ash or grayish brown, plain below, but on the dorsal side generally marked by numerous narrow longitudinal lines of brown pigment cells which give to that surface a generally brown effect. The entire preocular region is perfectly white, and the neural annuli, for most of the length of the body, are marked with two, four or six white spots arranged in regular longitudinal series and flanking the three or five rows of cutaneous papillæ which, owing to their black color, are by contrast very conspicuous. Sometimes the white spots fuse into metameric transverse bars and more rarely they are absent.

Habits—This handsome little leech is much less common than *G. stagnalis*, though in some localities it occurs in abundance along with that species and *G. complanata*. It seems to be more partial to colder waters than either of these species and is sometimes found in springs where they do not occur. In ponds it frequently fastens itself upon the shells of the larger species of *Lymnæa* and other snails and more rarely to the larger leeches. Less active than *G. complanata* it feeds less frequently upon active worms and larvæ but confines its attacks almost exclusively to the smaller snails.

In placing its eggs in a small number of large capsules this species resembles *G. complanata*, but it breeds later than that species, continuing far into the summer (as late as Aug. 6th) to carry newly laid eggs.

Concerning the name of this species it should be said that Verrill's name *lineata*, although the earliest, must be discarded on account of Müllers earlier use of *Hirudo lineata* which is clearly a *Glossiphonia* and probably *G. complanata*, though so far as I know it has been definitely determined. *Glossiphonia triserialis* E. Blanchard (1849) bears a remarkably close resemblance to our species and was at one time regarded by me as identical with it, but R. Blanchard has recently repeated (1900) his earlier statement (1896) that the genital orifices are separated by two annuli in this species and not by one as in *G. fusca*.



***Glossiphonia complanata* (Linnæus) Johnston.**

(Plate I, fig. 4)

*Hirudo complanata* Linnæus (1758)*Clepsine elegans* Verrill (1874)

Description—Although not much exceeding the species previously described in length when extended this leech is considerably larger and more bulky than any of them. The body is rather broad and flat with thicker margins, though *G. fusca* approaches it in this respect, and like that species it is incapable of great extension. In this connection it is interesting to note that both of these species have remarkably well developed longitudinal muscles. The head is not distinctly widened and the posterior sucker is small but powerful and less strongly directed ventrad than in the large species of *Placobdella*. There are at least four series of low, rounded but rather large cutaneous papillæ on which the dorso-median and dorso-lateral sensillæ are borne. There is no median series. Numerous small sense organs roughen the integument, which is rather opaque. A character which is quite unique among the *Glossiphonidæ* herein described is the presence of three distinct pairs of eyes situated on somites II, III and IV respectively. They are close together near the middle line and the pigment cups of the first are sometimes in contact, while the second are farthest apart and the largest in size. There is no nuchal gland.

Somites I and II are uniannulate, sometimes indistinctly separated; III is uniannulate or indistinctly biannulate; IV is biannulate, divided by a rather faint furrow into a larger anterior and a smaller posterior annulus. The next somite (V) is biannulate or more usually triannulate by the separation of *a1* by a shallow furrow from *a2*. Somites VI to XXIV inclusive are fully triannulate; XXV is biannulate and XXVI and XXVII usually uniannulate, the former frequently exhibiting some marginal division.

The mouth is of relatively large size and placed at the boundary between the second and the third somites. Like the closely related species the salivary glands are diffuse. Six or seven pairs of simple or slightly branched gastric cæca are present, the last reflected but relatively shorter than in the blood-sucking species of *Placobdella*. The longitudinal muscles of this species are remarkably powerful.

Unlike the three species of *Glossiphonia* described above the genital orifices of this species are separated by two annuli, the male

being situated at XI/XII, the female XII  $a_2/a_3$ . The vasa deferentia have the customary long posterior loops and enlarged sperm sacs. A very remarkable feature and one that is peculiar to this and a few very closely allied species is the presence of nine or ten pairs of testes in place of the six pairs usually present. The additional pairs are added at the caudal end of the series in somites XX to XXIII.

A more or less obvious narrowly striped pattern results from the more superficial pigments showing through the rather opaque integuments along the lines of the longitudinal muscles. The general effect is a somewhat heavy green or brown ground color marked dorsally and ventrally by a pair of very conspicuous longitudinal brown lines which above begin just behind the eyes while below they are slightly farther apart. The dorsal lines are broken into a series of short dashes by small metameric white or sulphur yellow spots corresponding with the dorso-medial papillae on the neural annuli. Four or five additional series of similar spots occur on the neural annuli, making six or seven in all. Of these the median series is the least constant, the others including the four constant papillae, to which two marginal series must be added.

Habits—The snail leech, as this species is named in England, abounds in certain localities in the shallows of rivers and large ponds, where it is found concealed beneath stones. It is remarkable among the small glossiphoniids for its great muscular strength, which enables it to overcome its prey and to adhere to stones with great tenacity. While more tardy in seeking to escape when disturbed than its most usual associate, *G. stagnalis*, it is more active in its movements when once aroused. It is more prone than most species to roll into a ball and may remain quiescent in this condition for a considerable period.

Although occasionally found attached to turtles the snail leech has not been observed to suck blood, but so far as my observations extend feeds exclusively in its natural habitat on small snails, worms etc., which its strength enable it to quickly overcome.

As usual the eggs are carried on the ventral side of the body and their large number, as well as the great length of the breeding season, render this one of the most satisfactory species for embryological study. It is one of the earliest as well as one of the latest of the Glossiphonias to bear eggs, which are contained in a small number of unusually large capsules.

**Genus *Placobdella* R. Blanchard.**

Body widened and moderately or excessively depressed. Suckers variable, the caudal sometimes with minute marginal serrations. Eyes usually one pair, compound, on somite III, rarely followed by several pairs of imperfect simple eyes. Cutaneous papillae variable, but usually numerous and some median. Pharyngeal salivary glands large and compact; gastric cæca seven pairs, very large and much branched in the flatter species. Sperm ducts without loops, compacted and much convoluted. Parasitic on turtles, fishes and batrachians, or free-living.

***Placobdella parasitica* (Say) Moore.**

(Plate I, figs. 7, 8)

*Hirudo parasitica* Say (1824)

*Glossiphonia parasitica* Castle (1900)

*Placobdella parasitica* Moore (1901)

Description—Of all of our numerous species of glossiphonids this attains the largest dimensions. Ordinarily examples are about two inches in length when extended, the giants upwards of four inches in the same condition. The form is broad, very flat and foliaceous particularly when food is absent from the cæca. In extension the head is somewhat expanded, but in contraction partakes of the general ovate pyriform outline of the body. The posterior sucker is of large size and considerably exposed behind the body, the plane of its adhesive surface being parallel with the ventral surface of the body. Cutaneous papillæ are numerous but inconspicuous, low and smooth; sometimes they are obsolete. The most constant are disposed in three longitudinal series on the neural annuli and two longitudinal series on the post-neural annuli. Those of the median series are not enlarged but on the contrary are usually smaller than those of the paired series.

The annuli and the somite limits are well defined, the furrows exhibiting certain constant differences in depth. Somites I and II are united in the reduced prostomial lobe, which may, but usually does not present a faint cross furrow; III and IV are triannulate, the anterior annulus in each case being much the larger. Somite V is triannulate dorsally but the furrow *a1/a2* is faint and becomes obsolete on the ventral side. There is a very gradual deepening of the furrow *a1/a2* on the succeeding somites, but VI to XXIII or sometimes

XXIV may be considered to be fully triannulate, as this furrow, though not so deep as the others, is complete. The first annulus ( $a_1$ ) is always more closely united with the second ( $a_2$ ) than is the third ( $a_3$ ). The furrows correspond closely on the dorsal and ventral surfaces. Somite XXIV is usually simpler, owing to the incompleteness of the furrow  $a_2/a_3$  toward the mid dorsal region. XXV is biannulate at the margins only, the furrows disappearing mesiad; XXVI and XXVII are normally uniannulate.

The small, pore-like mouth is in II. The salivary glands are compact and with a median lobe. As usual in this genus there are seven pairs of large spreading gastric cæca, in this species extensively developed and reaching almost to the margins of the body as fine lobes more numerous than in any other Minnesota species. The last pair is the largest and reflexed as far as somite XXII.

Small male and female orifices are located in the furrows XI/XII and XII  $a_2/a_3$  respectively. The testes are six pairs, the sperm sacs long but closely and complexly folded in somites XI and XII by the sides of the atrium.

The coloration is very rich and striking but extremely variable. The ground color of the dorsum is dull green, olive green or brown, marked with bright yellow which may replace the ground color very extensively. Usually the yellow is confined to the following regions:—A continuous or interrupted longitudinal median band which widens and narrows alternately at intervals of about three somites, regular marginal spots covering the intervals between the successive neural annuli, and large irregular blotches constituting an intermediate series which often become confluent with one another or with the marginal spots or both. The ventral surface is longitudinally striped with light and dark the whole having a peculiar bluish or purplish reflection. Dorsal integuments rather opaque.

Habits—Living chiefly as a parasite upon the snapping turtle on whose blood it feeds voraciously. The geographical range of this species is largely determined by that of its principal host. As the snapping turtle is an important article of commerce this leech is very well known and is reported from all parts of the United States. Its habits are too familiar to require description though it is not so widely known that the species also lives a free life particularly when carrying eggs or young and feeds on aquatic worms etc.

**Placobdella rugosa** (Verrill) Moore.

(Plate I, fig. 6, 9)

*Clepsine ornata* var. *rugosa* Verrill (1874)*Placobdella rugosa* Moore (1901)

Description—*Placobdella rugosa* is a large leech, nearly or quite equalling *P. parasitica*, although the great majority of examples met with average considerably smaller than that species. In form it is even more depressed, starving individuals being scarcely thicker than a card, very broad and leaf-like. The head is essentially similar to that of *P. parasitica* but as this leech does not extend itself as fully as that it is seldom seen in the distinctly expanded state. The caudal sucker is large and elliptical rather than circular, the antero-posterior diameter being slightly greater than the transverse. An important characteristic is the presence of numerous large rough cutaneous papillæ on the dorsum. The principal ones are constant in arrangement but the number of smaller ones is quite variable. Most characteristic and conspicuous are five on each neural annulus, median, supra-marginal and intermediate in position and forming five longitudinal series as far caudad as somite XXIII, posterior to which the median papillæ become greatly reduced in size and overshadowed by paramedian papillæ in line with the dorso-median sensillæ. On *a1* the papillæ are all relatively small while *a3* bears some of large size inferior only to the largest on *a2*. The integument is translucent.

Somites I and II are uniannulate and always distinctly separated; III is biannulate with a faint furrow usually discernible across the larger anterior annulus, on the posterior division of which are seen the small compound eyes, often included in a common pigment mass. Somite IV is triannulate dorsally but *a1/a2* is less distinct than the other furrows; V is triannulate dorsally, biannulate ventrally. The fully triannulate somites are VI to XXIII inclusive, and this species shows in a much less convincing way the transitional steps between biannulate and triannulate somites. In all of the complete somites a noteworthy feature is the lack of alignment between the dorsal and ventral furrows, as a result of which *a2* is the longest annulus dorsally but the shortest ventrally. Of the posterior simpler somites, XXIV is triannulate dorsally with *a3* of very much smaller relative size and incompletely separated

from *a2* on the ventral side, XXV and XXVI are wholly or partially biannulate and XXVII uniannulate.

The alimentary canal is nearly as in *P. parasitica* but the compact salivary glands have no median lobe and the divisions of the gastric cæca, although long, are less numerous. The reproductive organs are essentially similar in the two species, with the sperm sac, epididymis and ductus ejaculatorius compactly folded in somites XI and XII.

Owing to the numerous papillæ and the translucency of the skin the colors are a somewhat confused mixture of light and dark browns, yellows and greens, based upon a fundamental pattern similar to *P. parasitica* and consisting of a variegated brown ground with light intermetameric marginal spots, a median dorsal light stripe interrupted by short dark brown or brownish green longitudinal lines, which sometimes unite into a continuous dark line, and numerous small light yellow or green spots corresponding to the papillæ and sensillæ. The ventral surface is plain gray or light brown without longitudinal stripes.

Habits—*Placobdella rugosa*, the rough leech, is a very frequent inhabitant of streams and ponds, where it may be found clinging to the under side of stones and floating wood, especially during the late spring and early summer. At other seasons they are sometimes found upon aquatic turtles upon whose blood they in part subsist. Leeches of this species are sluggish and when exposed in their resting places press the flat body closely to the stone or log, whose colors they so closely simulate, and trust to this protective resemblance to escape detection, rather than creep actively away in the manner of many other species of allied leeches. The close resemblance to surroundings is much enhanced by the fact that particles of mud adhere to the mucous and rough papillæ. Furthermore the leeches may partially bury themselves in the bottom sediments. They seldom swim and when thrown into the water roll up and sink passively to the bottom, upon reaching which, they creep to a place of concealment in a most deliberate fashion.

So far as has been actually observed no other food than blood is taken though it seems probable that the juices and even the solid parts of small aquatic invertebrates may serve the same purpose, as is certainly the case in the nearest ally of this species.

The large chitimid spermatophores may be observed as frequently and easily as those of *P. parasitica* which they closely re-

semble in form and mode of fixation. The eggs are very numerous and are fixed lightly to the ventral surface of the body covered by a delicate mucoid membrane. During the period of incubation the parent leech attaches itself firmly and is very loath to leave its resting place. If, under such circumstances, force be used the leech holds tenaciously by both suckers to its support and curls the lateral margins of the body in such a manner as to enclose the eggs or young. As a result of a struggle to remove the brooding leech the eggs are generally detached and are then sometimes found to be adherant to the stone or glass of the aquarium against which they have been pressed. When forcibly removed from the eggs the leech will usually seek and return to them.

***Placobdella montifera* nom. nov.**

(Plate I, fig. 5, Plate II, fig. 10)

*Clepsine papillifera* var. *carinata* Verrill (1874)

Not *Clepsine carinata* Diesing (1858)

*Hemiclepsis carinata* Moore (1901)

Description—The size is moderate, never approaching the maximum of the two species of the genus already described. In addition to the widely expanded discoid head, which is quite characteristic, the form is more slender and less flattened and foliaceous than usual in the genus. The posterior sucker is large, circular, rather freely pedicillate and minutely denticulated about the margins. The oral sucker also possesses unusual mobility, has a prominent free margin all around and a narrow unsegmented border. The capacity for extension and contraction exceeds that of either *P. parasitica* or *P. rugosa*. The dorsum bears three rows of very large conical papillæ situated on the second and third annuli of each somite for the greater part of the body as far as somite XXI. These are borne on the crests of three prominent nearly continuous ridges. On somites XXII to XXVI the three tuberculated keels cease and are replaced by a pair of large paramedian papillae on each somite.

The anterior somites are better developed than in the closely related species, no doubt in correlation to the formation of the distinct head, into which the first five enter. The first two are each faintly biannulate, III is distinctly biannulate, with *ar* obscurely separated as a small anterior ring, behind which is situated the pair of small eyes. There are seventeen completely triannulate somites (VI to

XXII inclusive). In the neck-like constriction between the head and body is a peculiar double annulus which is interpreted as *V ar*. In the complete somites the three annuli increase in length caudad and  $a_3$  is partly cut into two by marginal furrows. Somites XXIII and XXIV are triannulate at the margins only, the third annulus of each being the least developed, and the furrow XXIV  $a_1/a_2$  deficient mesially. The two following somites (XXV and XXVI) are further simplified in the direction indicated in XXIII and XXIV. They are incompletely biannulate with only traces of  $a_2/a_3$ ; XXVII is uniannulate. Three well marked post-anal annuli form the narrow portion of the sucker pedicle.

The mouth is small in somite II; The proboscis is long and slender and the œsophagus of about equal length. There are the usual seven pairs of capacious gastric cæca divided into numerous lobes which reach almost to the margins of the body; the first sends a long anterior lobe forward into somite XI and the last reaches from XIX to XXIII. The salivary glands are compact and rather small.

While conforming in every important feature to the general plan characterizing the other members of this genus, the reproductive organs are somewhat peculiar in the shorter and more loosely folded sperm sacs.

The color is generally a dull greenish gray or pale olive brown with an interrupted dark green or brown median dorsal line, a series of obscure light yellow marginal spots or a marginal yellow border, more or less interrupted on the neural annuli, and spots of the same color, often including green flecks on the papillæ. A deeply pigmented green and brown spot marks the otherwise pale colored head. The ventral surface is plain.

Habits—This very interesting keeled leech exhibits little of that marked gregariousness which is common to most other members of the family. It is met with far more frequently singly than in company. As a parasite it devotes itself especially to frogs and, when they frequent the water during the breeding season, to toads.

It also habitually enters the shells of living mussels, though it is not known definitely that it feeds upon their soft tissues. Meadow brooks and swamps adjacent to the shores of lakes and ponds are its favorite haunts, where it lives among water plants and beneath stones as well as upon the bodies of frogs. Nothing is known of the breeding habits beyond the bare facts that spermatopores are deposited in early spring and that the young are carried:



Although Verrill was the first to describe this species, his name, which I used in a former connection when the species was erroneously referred to *Hemiclepsis*, is preoccupied by *Clepsine carinata* Diesing (1858) which is unquestionably a *Placobdella*. The name *montifera* is therefore proposed as suggestive of the resemblance of the carinæ to conventional mountain ranges.

***Placobdella pediculata* Hemingway.**

**Plate II, Figs. 13-18.**

*Placobdella pediculata* Hemingway, American Naturalist, Vol. XLII, 1908, pp. 527-532, figs. 1-3.

Description\*—Like *Placobdella parasitica* and *P. rugosa* this species reaches a large size, though no specimens quite equaling the largest examples of these, its allies, have been seen. Judged by the poor state of preservation of the few adults that I have examined it is in life soft-bodied and more than usually contractile. All of these specimens—numbering six—are gorged with blood and in this state are thick and hard in the region of the body occupied by the gastric cæca. All are strongly contracted and have the very characteristic pyriform outline and strongly convex dorsum evident in the figures, but the most striking peculiarity is the abrupt contraction and attenuation of the posterior segments to form a narrow pedicle supporting the caudal sucker, which, consequently, stands out freely exposed behind the wide posterior part of the body in a most characteristic manner. Hemingway has made the interesting discovery that this condition arises in the course of individual development and does not exist in young leeches one centimeter long, which consequently differ less obviously than do the adults from related members of the genus. The oral sucker, as far as can be determined in its contracted state with the lip inrolled, has the same structure as in *P. parasitica*.

The skin is perfectly smooth, without a trace of cutaneous papillæ; and only a few obscure segmental sensillæ and Bayer's scattered sense organs, the latter chiefly near the margins of the

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\*This description is printed substantially as originally prepared for this report but several important additions and corrections, for which I am indebted to Hemingway's paper, are either bracketed or specifically credited to that source.

body, were detected. Undoubtedly suitably preserved material would exhibit the sensillæ typically distributed and essentially as they occur in related species. Eyes are very difficult to detect in surface views of preserved adults but small pigment masses occur at III/IV in the same position as in *P. parasitica* and (distinct eyes appear at III/IV in the young). However, it has not been determined whether the eyes are simple or aggregated.

In spite of the obscurity due to great and often unequal contraction of the annuli a careful analysis of the external morphology shows that, except for the caudal peduncle and an apparently greater simplicity of corresponding anterior segments of *P. pediculata*, the structure is essentially as in *P. parasitica*. In respect to the annulation the condition existing in young leeches must be accepted with some caution as the somites become increasingly complex with growth and age. The annulation of somites I to IV of adults is unknown but in the young (I and II contain each but a single annulus and III and IV are biannulate). Somite V is biannulate dorsally but ventrally the furrow fades away toward the median line; VI is triannulate at the margins but the furrow a1/a2 is incomplete above and even more so below. Somites VII to XXIII (or XXIV) are triannulate but the furrow a1/a2 is incomplete medially on the venter of both VII and VIII and on most of the succeeding somites is less marked than either a2/a3 or the intersegmental furrows. On anterior somites, and, to a less degree on the posterior a3 is slightly longer than a1 or a2.

The annulation of the post-anal somites, constituting the caudal peduncle, is irregular and somewhat puzzling on the adult specimens, but here also most of the somites, while very short, appear each to be made up of three small annuli of varying size and incompletely defined limits. Figure 16 represents accurately the exact arrangement of the furrows. On young specimens (somite XXIV is triannulate, XXV, XXVI and XXVII are all biannulate but a1 of somite XXV is partially divided and a1 of both XXVI and XXVII is larger than a2). Somite XXIV, which immediately succeeds the anus, is the last segment of the body proper and on the contracted specimens its posterior border forms a fold which envelopes the contiguous portions of the narrow peduncle. The latter continues to taper to the sucker, to the middle portion of which it is strongly attached for rather more than the posterior half. The posterior sucker is large, circular and directed

strongly ventrad. (The disc is composed of somites XXVIII to XXXIV.) The few nephridiopores that are visible are situated as in *P. parasitica*.

The mouth is very small and is situated far forward near the anterior rim of the sucker in somite II. As in related species the proboscis is slender, the œsophageal glands compact and the stomach provided with seven pairs of large cæca reaching nearly to the margins of the body. The cæca are less deeply divided and simpler than those of *P. parasitica*, each of the first six pairs presenting only two or three rather short lobes. The intestine reaches to the posterior part of somite XXIV or even beyond and then bends abruptly forward toward the dorsum as an extremely narrow rectum to the anus situated at XXIII/XXIV. The forward curvature of the rectum and the anterior position of the anus are unique features in the family.

The reproductive organs are essentially similar to those of *P. parasitica*. The male and female external orifices are situated respectively at XI/XII and XII a2/a3. Six pairs of testes are crowded between the bases of the gastric cæca. The large sperm sac and ejaculatory duct of the vas deferens form a compact snarl in somite XII in the immediate neighborhood of the atrium.

In addition to the type specimen taken by Professor Nachtrieb from the isthmus of a sheepshead at Lake Pepin, the writer has also examined specimens in the collection of the Illinois State Laboratory of Natural History taken from the same host at Henry and Peoria, Illinois.

Habits—Hemingway gives the following account of what is known concerning the interesting habits of this leech:—

*Placobdella pediculata* appears to be a true fish parasite, having been found only in the gill chamber of the freshwater sheepshead (*Aplodinotus grunniens*), the posterior sucker of the leech being deeply imbedded in the side of the isthmus or shoulder. In the case of young leeches which have not been long attached, the depression caused by the posterior sucker is comparatively shallow, being a mere external depression in the inflamed tissues of the fish. As the attachment continues the inflamed tissues of the host grow up like a collar and close in around the leech's body in front of the sucker. This closing in of the inflamed collar presses upon the body of the leech, narrows it to a slender peduncle in front of the sucker and incidentally crowds the sucker down into the tissues of

the fish, so that, in time, this depression may reach into the underlying muscles of the host to a depth of half an inch or more and have an opening of about a quarter of an inch or less in diameter. The bottom of the depression has a larger diameter. Figure 5 of plate C represents the positions of three depressions from which the leeches have been removed, and figure 6 represents one of the depressions cut in two lengthwise.

These leeches are capable of becoming greatly contracted and when one is disturbed it draws back until it appears as a mere brownish pyriform knob which entirely covers the place of attachment.

The burying of the posterior segments in the tissues of the host has brought about an interesting structural change, so that we find the anal opening shifted forward to a position between somites XXIII and XXIV instead of between somites XXVII and XXVIII as in the other members of the genus. It is noticeable that, while the young leeches whose posterior portions are not yet deeply imbedded have the characteristic position of the anus (XXIII/XXIV), the outline of the posterior part of the body is still a regular curve showing none of the pedicular characteristics so pronounced in the older individuals. The posterior sucker, however, is very strongly developed even in those not more than a centimeter long.

Practically nothing is known of this leech separate from its host, but it seems possible that a part of its existence may be spent elsewhere. During September, 1903, I examined several thousand specimens of the sheepshead from Lake Pepin and found only three isolated leeches, each about a centimeter in length. The posterior sucker, while imbedded in the tissue, was not sunk in deeply and so had not produced the characteristic peduncel. They were evidently young ones which had recently attached themselves to their hosts and were gradually sinking the posterior sucker into the host's flesh. As full grown specimens, deeply imbedded, were found in the same locality during August of 1899, at least some of the adults must remain with their hosts during the summer and probably thruout the year.

**Placobdella hollensis** (Whitman)

(Plate II, fig. 11)

*Clepsine hollensis* Whitman (1892)

Description. This very distinct species will retain a permanent interest for zoologists because of its having furnished the material for Whitman's classical analysis of the nervous system of the leech. Its place in the fauna of Minnesota is established by several examples taken in Poplar Lake near St. Paul and sent to me with other leeches by Prof. Henry L. Osborn.

The form is very similar to *P. parasitica* but the present species is a very much smaller leech, a length of from one to one and one-half inches being about the usual size, though individuals reaching two inches in extension have been observed. The most obvious external characteristic is found in the eyes. As in other species of *Placobdella* a pair of large contiguous compound eyes exists in somite III with their bases resting in a conspicuous pigment mass and their principal visual component directed forward. But unlike the other species described this pair is succeeded by an indefinite number of pairs of much smaller eye-like organs which Whitman has shown to be the modified dorso-median sensillæ, which possess a diminishing number of visual cells in each successive pair toward the caudal end, and gradually pass into the ordinary sensillæ. Superficially each appears as a small clear or whitish area anterior to which more or less black pigment is accumulated in the form of an irregular cup. The first pair (on IV) is decidedly prominent and those on V and VI are also quite conspicuous and eye-like. At first sight, therefore, this might be described as an eight-eyed leech, with the first pair of eyes directed forward, the remaining three, which are smaller and simple, backward. More careful examination shows that the same features exist in a lessening degree in several additional pairs of the dorso-median and some of the dorso-lateral sensillæ as well, making it quite impossible to determine just where the visual possibilities of the sensillæ cease. All of the sensillæ are very distinct, rendering this a very favorable object for study on this subject.

The back is more or less roughened with small sense organs and a few larger round smooth papillæ. The latter correspond to the largest papillæ of *P. rugosa* and are most prominent posteriorly. In the Minnesota specimens they begin on the neural annulus of

VIII and by somite X present the following typical arrangement: The neural annulus bears a median one and a pair just mediad of the dorso-lateral sensillæ.  $a_3$  bears a pair directly in line with the dorso-median sensillæ and  $a_1$  a smaller median one.

This species exhibits the same gradual development of the biannulate and triannulate somite as *P. parasitica* and consequently presents the same difficulties in the application of a formal descriptive terminology. Somites I and II may be considered as uniannulate, III, IV and V as biannulate, VI as transitional and VII to XXIV or XXV as triannulate; XXVI and XXVII exhibit partial subdivision only at the margins. The complete somites of the middle region of the body show the same tendency of the sub-division of  $a_1$  and  $a_3$  into secondary annuli that is exhibited by *P. rugosa*. In the internal anatomy a considerable number of minute differences between this species and *P. parasitica* have been observed, but the general and obvious structure of the alimentary canal and reproductive organs of the two species is essentially alike.

The colors as described from living eastern representatives of the species are rather characteristic. The dorsum is generally a light olive green variegated with brown, pale yellow, and colorless areas. The head end lacks pigment almost entirely except what is concentrated about the eyes and in the transverse bands on the neural annuli. This light area extends caudad for some distance as a median vitta between the pairs of small eyes. On the neural annuli it is usually interrupted by the transverse bands of interocular pigment between which it is flanked by dark cloudings which more posteriorly takes the form of a pair of dark longitudinal bands just mediad of the dorso-median sensillæ. At about somite X and thence caudad, the median vitta and its dark flanking bands are transformed into a chain-like pattern consisting of alternate dark bars and elliptical rings with light centers, the former extending over about two somites and the latter one somite, there being about five of each. Posteriorly an elongated light median area represents several of the rings coalesced.

The larger cutaneous papillæ are of a light yellow or cream color and those of the most medial neural series interrupt the dark bands described above. A similar yellow color occurs along the margins, alternating in blocks with the green ground color. In many specimens narrow bands of dark pigment extend across the entire dorsum of the anterior neural annuli and less frequently all or nearly all of the sensillæ are flanked on the medial side by brown or black pigment. The ventral surface is nearly plain.

**Habits.** This very interesting leech bears the same relation to the smaller fresh water tortoises that *P. parasitica* does to the snapping turtles and other large species. Not every tortoise is parasitized but as a rule several of the leeches are found associated together on each one so affected. The species also frequently occurs on the under side of floating wood in ponds inhabited by tortoises. In its movements it is more active than other species of *Placobdella* and swims with much greater facility than any other, not excepting *P. montifera*. The spermatophores and breeding habits are very similar to those of *P. parasitica* and *P. rugosa*.

**Genus Hemiclepsis** Vejdovsky.

Form variable, usually rather wide and moderately depressed; tissues soft and almost œdemous, translucent. Suckers as in *Glossiphonia*. Eyes usually four pairs, in longitudinal series near the median line. Cutaneous papillæ few and low. Pharyngeal salivary glands diffuse; gastric cæca nine or ten pairs, branched. Genital pores as in *Glossiphonia*, but sometimes farther apart. Chiefly free-living.

**\*Hemiclepsis occidentalis** (Verrill)

(Plate II, fig. 12.)

*Clepsine occidentalis* Verrill (1874).

**Description**—This rare and very interesting leech is represented in the Minnesota collection only by a batch of young, evidently removed from the parent which carried them, and is consequently described from specimens received from other localities, though the anterior end of one of these young is represented in the figure. The leech is of moderate size, about one and one-half inches being the limit in extension. In life it is of a rather slender form, broadly rounded anteriorly where there is no definitely expanded head, moderately depressed but rather thick at the margins posteriorly and with a very large caudal sucker. A noteworthy feature which separates this from every other species described in this paper is the peculiar transparency and gelatinous consistency of the body.

There are four pairs of large conspicuous eyes, which cannot be mistaken for the much smaller ones of *Placobdella hollensis*. They are situated on somites II to V respectively; the first pair is the

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\*The name *Protoclepsis* Livanow (1902) proposed for this group is pre-occupied by *Protoclepsine* Moore 1898.

smallest and very close together or even in actual contact, the others are successively more distant and the third pair is the largest. The first and second are directed forward and outward, the third and fourth backwards and outward.

The upper lip is very mobile and in preserved examples is almost invariably curled into the cavity of the sucker. The small mouth is far forward in somite II. Genital orifices occur at the positions so frequent in the *Glossiphoniidae*, the male at XI/XII, the female at XII  $a_2/a_3$ . In one specimen the male bursa is everted in the form of a short conical penis, this being the only species of the family described in this paper in which such an organ is present.

Besides the numerous scattered sense organs which roughen the skin there are three pairs of low dome-shaped papillæ on each neural annulus except at the anterior end of the body. Apparently these bear the dorso-median, dorso-lateral and dorso-marginal sensillæ, the first of which are separated by about one-fourth of the width of the body.

With the exception of somites X, XI and XII, on which they cannot be detected nephridiopores occur on  $a_2$  of every somite from VIII to XXV. Very little is known of the internal anatomy of this species but quite enough to establish its position as a member of the genus. The proboscis is very short and is succeeded immediately by a very short œsophagus and a long stomach which bears nine pairs of branched cæca, two of which are anterior to the reproductive orifices and the last reflected in the usual manner. The muscular system is very peculiar in the wide intervals which exist between the bundles of muscle fibers.

The color of preserved specimens is a translucent grayish green, the dorsum being rather thickly spotted with cream yellow, the largest spots corresponding with the six series of papillæ described above.

The annulation presented in figure 12 should not be taken as fully characteristic of the species as it exhibits the somites in the undeveloped biannulate or nearly biannulate condition which is observed in the young of all species. With a more pronounced development of the furrows between  $a_1$  and  $a_2$  it would, however, be diagnostic. In the adult somite I is a distinct but small preocular lobe, II nearly and IV fully biannulate. A very interesting feature, which is found in all of these young and in the few adults which I have studied, is that somite V is shorter and much less elaborate than IV. Somite VI approaches the triannulate type very closely and VII to XXIV inclusive



are completely triannulate; their annuli and furrows are all equal. Finally XXV is biannulate, XXVI biannulate or uniannulate and XXVII uniannulate.

It is not at all certain that this is really Verrill's *Clepsine occidentalis* as at least two and perhaps three other species of eight-eyed glossiphoniids are found in this country.

Habits—An eastern species of *Hemiclepsis* has been observed in the living state and it is probable that the habits of the form described will not depart much from this. The most striking peculiarity is its remarkable activity. No other members of the family creep with anything approaching its speed. In creeping the caudal sucker is brought forward into actual contact with the oral sucker and the movement is repeated with great rapidity. So far as has been observed the species is entirely sanguivorous, the blood of frogs being taken while worms and snails are refused. The European *H. tessellata* is known to attack water fowl and to be transported while attached to their legs or within the nasal chamber which it occasionally enters. Fertilization takes place by means of spermatophores attached to the skin, but egg laying has not been observed.

#### Family Ichthyobdellidæ.

Leeches of small, medium or large size. Form much varied; short and stout or elongated and slender, terete or depressed, usually more or less divided into a narrower anterior and an expanded posterior region. No distinct clitellum, but diffuse clitellar glands abundant. Segments smooth, or more rarely papillated, often provided with lateral pulsating vesicles or gills on a certain number of segments. Complete somites with from 2 to 14 annuli, greatly varied in proportions. Both oral and caudal suckers usually large and deep and more or less prominently set off on pedicles. Eyes 1 to 3 pairs widely separated on posterior part of head, often absent. Eye spots often on caudal sucker. Mouth and proboscis as in *Glossiphoniidæ*; stomach straight and usually simple, only rarely with lateral cæca, one pair of large posterior gastric cæca, variously and sometimes completely united. Genital orifices much varied in position according to the number of rings per segment. Testes usually five or six pairs, the sperm ducts relatively short, the epididymis and ejaculatory duct not much convoluted, ending in an atrium that may be simple or more or less complex; no filiform penis. Ovisacs paired or united into one, pyriform or globular, their ducts simple. Eggs laid in usually stalked

cocoons. Chiefly semi-permanent parasites on fishes, sometimes on crustaceans. Nearly all are marine. *Piscicola* and closely related genera only are found on fresh water fishes.

### Genus *Actinobdella* Moore.

Rather slender and elongated, moderately depressed or half round. Oral sucker slightly developed; caudal sucker large, deep, and provided with a circle of numerous marginal papillæ and glands. A few dorsal papillæ, some median. Complete somites of six unequal rings. Eyes, one pair on III, united. Pharyngeal salivary glands diffuse; gastric cæca seven pairs, branched. Genital orifices separated by four rings; sperm ducts lacking long loops, moderately compact. Small blood-sucking leeches, probably parasitic on fishes.

### *Actinobdella inequiannulata* Moore.

(Plate III, fig. 19, 20.)

#### *Actinobdella inequiannulata* Moore (1901)

Description—The collections from Lake Pepin included an example of this very interesting species, the second one known, which enables me to confirm and extend, and in some particulars to correct, the original description. This additional knowledge renders more evident than before the position which *Actinobdella* occupies on the border between the two families of *Ichthyobdellidæ* and *Glossiphoniidæ*, in fact the mere numerical weight of its characters as now known point rather toward an alliance with the latter. As I hope soon to have sufficient material to permit a thorough anatomical study the discussion of its zoological position can best be postponed. The Lake Pepin specimen measures 12 mm. in length and has nearly the form of the type except that the middle region of the body is somewhat widened. The following description is nearly a transcript from the original with such changes and additions as further knowledge necessitates.

The form is slender and depressed throughout, with the dorsal surface convex, the ventral flat and the margins sharp. The breadth is nearly equal or somewhat greater in the middle region, but contracts suddenly at the posterior end to constitute the narrow pedicle of the conspicuous caudal sucker, and at the anterior end tapers gently to the broadly rounded upper lip.

There is no conspicuously expanded anterior sucker or head as in typical ichthyobdellids, but this end of the body is formed exactly

in the fashion of a glossiphonid. Four somites of simple structure enter into its composition, the posterior ventral rim being formed by the fourth and fifth somites in that region largely coalesced. On the middle of somite III is situated the single pair of small eyes conjoined in a single median pigment mass and looking forward and outward. Some detached pigment cells occur caudad and lateral of this position.

Most remarkable of all of the external features of this leech is the posterior sucker. It is much wider than any part of the body, largely free around its entire circumference and supported by a narrow central pedicle. The ventral surface is very deeply cupped and the rim somewhat contracted, making the diameter of the opening somewhat less than that of the internal cavity. From the internal face of the sucker, a short distance back from the sharp margin, spring about thirty (thirty in one, twenty-nine in the other, specimen) slender finger-like papillæ which project more or less freely beyond the margin. Owing to their contractile nature they vary in length and diameter but when extended the longest are about .4 to .5 mm. in length and about .1 mm. in diameter. Each one contains an axial gland duct or group of ducts surrounded by a sheath of muscle fibres which spring from the muscular ridges passing radially down the inner face of the sucker. The gland ducts arise from a circle of glands which appear as a circle of whitish spots arranged around the sucker about midway between the margin and the pedicle and which raise the outer surface into a slightly marked encircling ridge.

A median series of rather prominent conical papillæ with the long diameter of their elliptical bases directed in the longitudinal axis of the leech occur on the large annuli *b*<sub>3</sub> and *b*<sub>5</sub>. In the Lake Pepin specimen these papillæ begin on VIII *b*<sub>5</sub> and continue to XXVI *b*<sub>3</sub>; in the type they are distinctly developed only on the somites XI to XXV inclusive. In the new example also traces of supra-marginal and intermediate series of papillæ are found on the somites of the middle region. Segmental sensillæ are very beautiful and regularly shown in this specimen on all of the somites and both dorsally and ventrally. The position of those found in the type and shown in the figure of that specimen is confirmed and in addition the presence of supra-marginals and of six ventral series is established. Thus it will be seen that the sensillæ have the arrangement characteristic of the *Glossiphonidæ*. Well developed rings of small sense organs are visible on annuli *b*<sub>2</sub>, *b*<sub>3</sub> and *b*<sub>5</sub> of each of the complete somites and are more or less discernible on all primary annuli and more comprehensive divisions throughout the body.

Somites I, II and III are each uniannulate; IV is also practically uniannulate but shows some signs of division above in the Pepin example and below is largely united with V. The latter, together with VI and in the type, VII also, is biannulate, an interesting feature being the rather larger size of second annulus. Somite VIII is quadriannulate, being composed of  $a1/a2/b5/b6$ , the latter two being very narrow.

Somites IX to XXV inclusive may be regarded as complete, but some individual variations are exhibited and especially the first two and the last are transitional. In the original specimen the complete somites are sexannulate, the full number of secondary annuli being developed, but of very unequal size. Two annuli, ( $b3$  and  $b5$ ) are enlarged, the latter most so, and bear the dorsal cutaneous papillæ, and the former the metameric sensillæ as well;  $b1$ ,  $b2$  and  $b6$  are about equal and  $b4$  is the smallest of all. The small annuli  $b1$ ,  $b4$  and  $b6$  appear to be entirely unadorned, while  $b2$  like the large papillated annuli exhibits a circle of sense organs.

The conditions in the new specimen are essentially similar, but the somites are somewhat further elaborated. Somite VII is triannulate rather than biannulate, VIII has the small annuli  $b1$  and  $b4$  rather distinctly separated and there is a very strong tendency in the anterior part of the post-clitellial region toward the splitting off of small additional annuli from the anterior margins of the enlarged annuli  $b3$  and  $b5$  which leads toward the production of octannulate somites. A trace of this is indicated in some of the somites of the type specimen as is shown in the figures.

The remaining pre-anal somites XXVI and XXVII are typically triannulate. Two post-anal annuli are present in the type and four in the new specimen.

A few anatomical facts gleaned from the Lake Pepin specimen, though very fragmentary, are nevertheless of great interest; for it will be seen that in all essentials the alimentary canal is constructed on the plan prevalent in the *Glossiphoniidæ*. The position of the mouth at the extreme anterior margin of the oral sucker in somite II, or perhaps even in I, is paralleled in the *Ichthyobdellidæ* only in *Notostomum* (Levinsen 1881). The proboscis is long and slender, reaching when retracted, from VI to X, at its posterior and receiving apparently three pairs of slender ducts from the salivary glands. The latter consist of very numerous small gland cells scattered diffusely all through the preclitellal somites as far as the head. The œsophagus

is slender and distinctly differentiated from the stomach. At least six pairs of well marked, long and slender gastric cæca are developed, arising in somites XIV to XIX inclusive. Unfortunately they are empty and shrunken and on account of the numerous gland cells which fill the region difficult to see clearly, but they are certainly somewhat branched and extend far toward the margins of the body. Those of the last pair are long and reflected and extend as far as XXII, lateral branches arising in each intervening somite in the characteristic glossiphonid fashion. The intestine is a narrow tube which gradually tapers to the anus and shows the differentiations usual in the higher glossiphonids, including four pairs of prominent slender cæca which arise in somites XX to XXII and lie dorsad of the last pair of gastric cæca. The first two are bent forward, enlarged at the end and somewhat subdivided, the third is bent backward and slightly lobulated and the last is simple and directed rather strongly caudad from its origin. The anus is situated at the posterior margin of XXVII, in this case within the limits of that somite.

Very little of value can be made of the internal genital organs. The testes are not certainly discernible. There is a pair of short wide sperm sacs crowded with spermatozoa extending from the posterior limit of somite XIII to a point just abreast of the male bursa, where they pass into the narrower ejaculatory ducts which curve around the anterior face of the bursa toward the median plane and then bend dorsad and caudad to the summits of the prominent nearly spherical prostate cornua. The latter open on each side into the dorsum of the small bursa. The ovaries are enlarged pyriform bodies which lie rather widely separated just caudad of the sperm sacs; from their anterior enlarged ends narrow oriducts pass mesiad and slightly cephalad to the female orifice. The external genital orifices are situated in the positions usual in the higher *Glossiphonidæ*, the male at XI/XII, the female approximately at XII *a*<sub>2</sub>/*a*<sub>3</sub>. Nephridiopores are quite easily distinguishable on the post-clitellal complete somites just anterior to the sensillæ line on annulus *b*<sub>3</sub> and well mesiad of the margins.

According to the label the Minnesota specimen was colored green during life. It was pumped from the bottom of Lake Pepin. Nothing is known of the habits of this leech.

**Genus *Piscicola* Blainville.**

Size small; form slender and elongated, terete or subterete. Both suckers large and explanate, the posterior usually deeply cupped. Complete somites of 12-14 very short tertiary annuli. Sensillæ and cutaneous papillæ very inconspicuous or absent. Eyes one or two pairs widely separated on base of "head". Atrium simple and intestinal cæca nearly completely coalesced. Parasitic on fishes, but often found free.

***Piscicola punctata* (Verrill).**

(Plate III, figs. 21, 22)

***Ichthyobdella punctata* Verrill (1871)**

Description—The usual size of this species is from 15 to 25 mm. long and 2 to 3 mm. in greatest diameter, but the largest examples are capable of extending to a greater length. In extension the body is circular in cross section and very slender, widest at the beginning of the posterior third. When contracted the distinction between anterior and posterior regions of the body is much emphasized and the latter becomes distinctly flattened. Although it has the form characteristic of the genus the head is much smaller than in the well known *P. geometra*.

Only one pair of eyes has been detected in a large number of specimens which have been received from various localities. These have conspicuous pigment cups situated in somite four and consequently correspond to the posterior eyes of *P. geometra* which they resemble also in the fact that they look caudad instead of cephalad as do the first pair in that species. The smaller posterior pair described by Verrill I have been unable to find either in entire mounts or in sections and it is possible that some of the conspicuous pigment cells which are scattered through the head may have simulated eyes in his living specimens.

During life the posterior sucker is widely expanded and hemispherical, but in preserved specimens it is always much contracted and directed caudad. Just anterior to it is the minute anus among a group of small wrinkled annuli.

The genital region (clitellum) is more or less distinctly limited by anterior and posterior constrictions at the furrows IX/X and XII/XIII respectively. In contraction XII may be more or less retracted within the anterior border of XIII and all three of the somites

of this region are of simpler structure than the typical complete ones adjoining. Clitellar glands are greatly developed and form a thick layer just within the longitudinal muscle layer and extending from the clitellum nearly to the anus. They are arranged in four longitudinal bands on each side leaving narrow neural, median dorsal, and lateral spaces clear. The latter are occupied by the lateral vessels which exhibit metameric enlargements in the somites of the posterior region.

Ten pairs of large nephridiopores are present on the latero-ventral region of somites XIV to XXIII inclusive. They lie in annulus c6. No especially metameric sensillæ have been certainly distinguished but numerous small sense organs arranged in transverse rows in many of the annuli are present.

Owing perhaps to the different methods by which my material has been prepared the annulation varies in a manner which, combined with its complexity, is very confusing, and a complete analysis has not been reached. Figure 21 Plate III exhibits a case which approximates the most frequently occurring condition, together with the interpretation of somite limits which has been based upon a study of the annuli themselves, the nephridiopores, nerve ganglia and partially of the peripheral nerves.

Complete somites have the full number of tertiary annuli (c1 to c12) developed and in many one or two of these, usually in the cephalic third of the somite, are divided into two, making in the latter case fourteen annuli; but it is in connection with this feature and the simpler somites at the ends of the body that the variability occurs.

Unlike *Actinobdella* the mouth is situated far back in the oral sucker at III/IV or possibly within the limits of IV. The rather short proboscis ends in VIII where it receives the several ducts of the diffuse salivary glands occupying the pre-clitellial region. The stomach is moniliform, constricted into six spheroid chambers occupying somites XIV to XIX inclusive and entirely without lateral cæca. The last one passes into a long capacious unpaired cæcum which shows no apparent traces of its dual origin and extends with slight sacculations to a point immediately beneath the anus. The stomach and cæcum, as might be expected, have a precisely similar histological structure and both have a green color owing to the presence of numerous branched pigment cells in their walls. The intestine arises from the dorsum of the last gastric chamber in XIX by a constricted opening and lies dorsad of the cæcum throughout its length. At its commencement it bears a pair of short wide pouches which project for-

ward. About its middle is a constriction and caudad of this an enlargement bearing another pair of cæca. Smaller cæca may occur between.

There are but five pairs of testes alternating with the gastric sacculations. Very delicate vasa efferentia start at the dorso-mesial side of the testes and then pass forward and outward among the ventral clitellar glands to the vas deferens, a very delicate tube resting on the ventral body walls. Passing ganglion XIV the vas deferens becomes larger and its course wavy and just in front of ganglion XIII expands into a short, wide sperm sac which is looped caudad and, after a constriction passes into a ductus ejaculatorius of half its diameter and twice its length. The latter becomes very narrow as it enters the thick loose layer of unicellular glands which conceal the median ever-visible bursa from view. The male orifice is located at XI/XII. The paired ovaries are large elongated simple sacs which even in their much folded condition reach as far caudad as somite XVI. They open at or about XII *a2/a3*.

Verrill describes the colors during life as "translucent greenish, with a pale median dorsal line and with minute black specks arranged in transverse bands; along each side are eight light spots, alternating with the dark punctate bands." The black specks are branched pigment cells which are scattered through the integument with singular regularity. Large individuals become more opaque owing to the great development of clitellar glands.

Habits—This is our commonest fresh water fish leech. It is common in the ponds and lakes of the northern states and the Mississippi Valley and is especially abundant along the Ohio shore of Lake Erie. It lives upon the exterior of the body of various species of small fishes feeding upon the mucous which covers the surface as well as upon their blood. It appears to be in no way injurious to its hosts. Many examples may also be found living among water plants to the stems of which there is good reason to believe its stalked cocoons are attached.

### Family Hirudinidæ.

Leeches mostly of large size, more or less elongated, with thick, little depressed bodies. A well-developed zonary clitellum in most species during the breeding season. Oral sucker forming lips surrounding the large mouth; caudal sucker rather small or well developed, discoid. Complete somites usually of 5, rarely of 3 or 7, an-



nuli. Eyes usually 5 pairs, forming a marginal arch on somites II to VI. Metameric sense organs usually conspicuous colorless spots on the neural annuli, 6-8 above and 4-6 below. Cutaneous papillæ small or absent. Mouth large, occupying entire oral sucker; pharynx not protrusible, usually preceded by three compressed, muscular, toothed jaws, one dorsal and two ventro-lateral, the former alone, or all three sometimes absent. Stomach with a single posterior pair of simple cæca, or provided with one or two pairs of cæca in each segment; no intestinal cæca. Genital pores variable, the male usually on XII, female on XIII and usually separated by 5 annuli; associated copulatory glands may be present. Testes sacs usually 10 pairs belonging to somites XIV-XXIII. Genital ducts complex, the male terminating in an unpaired atrium with prostate gland and a usually filiform penis. Ovisacs 1 pair, small pyriform, opening into an unpaired oviduct terminating in a long vagina. Copulation occurs, during which the penis of one individual implants spermatophores in the vagina of the other. Eggs enclosed in vesicular or spongy chitinous cocoons deposited in damp earth. Fresh water or more rarely terrestrial leeches, which are voracious blood suckers or predatory destroyers of weaker invertebrates. Mostly active swimmers.

#### Genus *Macrobdella* Verrill.

Size large. Dorsum marked by metameric red and black spots. Jaws prominent each bearing numerous small teeth in a single series; gastric cæca very spacious, two pairs to each somite from X to XVIII. Genital orifices separated by from  $2\frac{1}{2}$  to 5 rings, followed by the two pairs of copulatory gland pores, which form a quadrate figure opening in the furrows XIII/XIV and XIV *b1/b2*; penis short and conical; atrium and vagina both short, globoid. Active blood-suckers, attacking vertebrates.

#### *Macrobdella decora* (Say) Verrill.

(Plate IV, figs. 24, 25; Plate V, fig. 38)

*Hirudo decora* Say (1824)

*Hirudo decora* Leidy (1868)

*Macrobdella decora* Verrill (1872)

Description. *Macrobdella decora*, the American medicinal leech, reaches a length of eight to ten inches and a breadth of three-quarters of an inch, but the examples most frequently met with are much smaller than this, while the largest may occasionally exceed this size.

The body is depressed throughout, more so than in any native species of the family and the margins are sharp. During life, however, the body is very soft and assumes a great variety of attitudes and shapes.

The oral sucker is a powerful organ provided with a rather wide unsegmented and very mobile border which very materially increases its extent. Anteriorly a distinct median emargination corresponds with a deep ventral sulcus which divides the upper lip and is flanked by a pair of somewhat shallower sulci. The upper lip can be folded into the buccal chamber and almost concealed by the lateral lobes which close beneath it. As usual in the family there are five pairs of eyes, larger in this species than in the species of *Hæmopsis*. Their arrangement is sufficiently indicated in the figure. The posterior sucker is large, broadly attached and circular.

When fully developed the clitellum is firm and thick and extends over eighteen annuli, from X *b*<sub>5</sub> to XIV *b*<sub>2</sub>, but it is seldom so well marked nor so extensive. In the ordinary condition the male pore appears as an opening of considerable size in the furrow XI/XII, into which the surrounding regosities converge. When these inflected parts are everted they form a more or less prominent conical penis which reaches a length of about three millimeters when fully protruded. In this condition it is supported almost entirely on annulus XII *b*<sub>1</sub> which has greatly encroached on the preceeding annulus in the middle region. The female orifice is a small opening with rugous margins situated at XII/XIII or XIII *b*<sub>1</sub>.

Very characteristic of the genus are the copulatory glands, which form conspicuous masses occupying a large part of the middle region of the floor of somites XIII and XIV. Their external openings are four in number, arranged at the four angles of a nearly square figure, the first pair opening in the furrow XIII/XIV and the second in the furrow line XIV *b*<sub>1</sub>/*b*<sub>2</sub>. Surrounding each of the pores is a slightly tumid region extending over the contiguous halves of the two annuli between which the pore lies. When fully developed the four tumosities are separated only by shallow furrows and together form a conspicuous rugous quadrate area extending over the posterior half of XIII *b*<sub>6</sub>, the anterior half of XIV *b*<sub>2</sub> and all of the intervening annulus. Longitudinal and transverse diametral furrows divide it into quarters.

The surface of the body of this species is quite smooth and free from papillæ, although more or less roughened in some preparations by the scattered sense organs. Nephridiopores and sensillæ have the

customary disposition. The latter can be very favorably studied on the dorsal surface but are difficult to distinguish on the generally light background of the ventral surface.

Somites I, II and III are uniannulate, IV and V biannulate, and VI triannulate on the dorsal side. Somites VII and VIII are respectively triannulate and quadriannulate but VII *a*<sub>3</sub> and VIII *a*<sub>1</sub> are enlarged and quite distinctly subdivided dorsally. Then follow sixteen complete quinquannulate somites, IX to XXIV inclusive, in which the neural annulus is typically shorter than any of the others. At the posterior end XXV is again quadriannulate, there being only one post-neural annulus (*a*<sub>3</sub>) instead of two, XXVI is biannulate with *a*<sub>1</sub> more or less distinctly separated from *a*<sub>2</sub>. The large anus cuts into the posterior margin of XXVII.

As in all of the predatory leeches of this family the mouth is of large size and may be considered to be coextensive with the opening of the oral sucker. The three jaws exhibit the usual relations, but their form is characteristic of the species among the leeches of the northern United States. They are about twice as long as high and each bears about sixty-five fine conical, slightly retrorse, uniserial teeth. A very short pharynx with several longitudinal folds reaches to about IX, within which segment it is succeeded by a still shorter œsophagus which can scarcely be distinguished from the stomach, as sacculations begin to be evident immediately. From X to XVIII inclusive each somite includes two pairs of gastric cæca of which those from XIII backward are of large size. The last pair, which originate from the stomach in the anterior part of somite XIX, are of very great extent, reaching XXIV or XXV, and bear two wide lateral branches in each of the intervening somites. The straight narrow intestine presents no noteworthy features.

Ten pairs of testes are situated, intermetamerically, as most usual in the leeches, at XIII/XIV to XXII/XXIII inclusive. The vasa deferentia are enveloped in crowded unicellular glands and follow somewhat sinuous courses. In somite XI they lose their glandular covering and appear as delicate ducts, which opposite to ganglion XI pass abruptly into the anterior end of the compact massive epididymes. From the posterior end of the latter wide somewhat folded ducti ejaculatorii lead to the terminal organ. Just before entering the outer glandular covering of the bursa or atrium the ducti become constricted and then rise as a pair of slightly enlarged sacs which open into the summit of the invaginated bursa to which they stand in the relation

of cornua. This median organ which evaginates to form the penis is in its retracted condition spherical or inverted pyriform and has thick muscular and glandular coats.

The colors during life are very showy. Above the ground varies from a light sage green to a rich olive green with obscure longitudinal stripes or short lines in the median areas. The median metameric spots are cadmium orange or light red and the marginal spots black. The ventral surface is a rich orange sometimes plain, sometimes spotted with black. The colors fade very quickly in alcohol.

Habits—This species, the native American medicinal leech, approaches closer to the European *Hirudo medicinalis*, both in structure and habits, than any other indigenous American species, and, when the use of leeches for blood-letting was more general than now, was largely employed by physicians. To a limited extent it is still gathered in the swamps below Philadelphia and sold for this purpose. It is widely distributed throughout the northern half of the United States and in Canada and is an inhabitant of standing water rather than of streams or rapidly flowing rivers. Great numbers often occur in small ponds and lakes. Altogether it is the best known of the American leeches and has been frequently written about since its discovery by Say in 1824, but its exterior has not hitherto been figured although Whitman has published drawings of the annulation of a closely allied species.

*Macrobdella* is more strictly aquatic than the species of *Hæmopsis* and probably does not leave the water voluntarily though it will live for weeks buried in the mud left by the drying up of small ponds and pools in dry summers. It is an active predacious creature and swims actively at the surface at night or during the day if attracted by the presence of food. It is well known to the American boy who frequently comes from his plunge in the brickyard or meadow pond with several of these leeches firmly attached to his skin, an experience so frequent as to have gained for it the general name of blood-sucker.

It also attacks cattle which enter its domain to drink or cool but its natural food is the blood of fishes, frogs and turtles which it attacks and frequently kills. Small aquatic annelids in large numbers and occasionally larval insects have been found in the stomach. In the spring frogs eggs are devoured in large numbers, the eggs being sucked out after the gelatinous envelopes have been cut by the sharp saw-like teeth of the leech.

In coitus the leeches cohere by means of the secretion of the copu-

latory glands at the same time coiling somewhat about each other. Cocoons are formed and deposited in the mud by the side of the pond, and there left to hatch.

**Genus *Hæmopsis* Savigny.**

Size large to very large. Dorsum plain or marked by a median stripe or by irregular non-metameric spots and blotches. Jaws small and bearing a few large double teeth, or absent; one pair of posterior gastric cæca only. Genital pores separated by five rings; no copulatory glands; penis filiform; atrium and vagina both much elongated. Food chiefly worms, insect larvae, etc., not normally blood-suckers.

***Hæmopsis marmoratis* (Say) Moore.**

(Plate IV, fig. 32)

*Hirudo marmorata* Say (1824)

*Aulastomum lacustre* Leidy (1868)

*Haemopsis marmoratis* Moore (1901).

Description—The size is medium, seldom exceeding six inches in length and one-third of an inch in diameter, though larger specimens are sometimes met with. Owing to the extensive development of botryoidal tissue the body is exceedingly soft and limp and consequently varies greatly in shape. Compared with the other species of *Hæmopsis* described in this paper the form is rounder and less flattened than they, except in swimming, when this species also becomes flattened.

Although the anterior sucker is relatively large and the lips broad, the unsegmented margin is very narrow and there are no distinct inferior sulci as in *Macrobdella*. Of the five pairs of eyes the first three pairs are conspicuous and are arranged in a regular arc on the first three annuli; the fourth and fifth are on the sixth and ninth annuli respectively and are much more obscure, being deeply placed. All of the eyes are smaller than the corresponding ones of *Macrobdella*. In mature individuals the clitellum is very distinct and equally well developed dorsally and ventrally and often is the widest region of the body. It extends over fifteen annuli, from X *b*<sub>5</sub> to XIII *a*<sub>2</sub> inclusive. The posterior sucker is relatively small, circular and broadly attached; about one-third of it projects beyond the body posteriorly and its anterior margin reaches to XXV *a*<sub>2</sub>.

Somite I can seldom be distinguished from II which again is imperfectly separated from III; IV is biannulate, as is V also, but the

latter is more fully elaborated dorsally. On the typically biannulate somite VI,  $a_1$  and  $a_2$  are more or less separated by a furrow confined to more or less of the middle dorsal region. Somite VII is fully triannulate but is peculiar in the large size of  $a_3$ , which, moreover, may exhibit a faint dividing furrow; VIII is quadriannulate and  $a_1$  resembles VII  $a_3$  in being enlarged and partly subdivided. There are fifteen (IX to XXIII) quinquianulate somites, in which all of the annuli are approximately equal. Somite XXIV is quadriannulate and sometimes the last annulus ( $a_3$ ) is faintly subdivided, usually on the ventral surface; XXV is triannulate, but  $a_1$ , which is normally of larger size than the remaining annuli, is subject to much variation. The following two somites, XXVI and XXVII, are variable and difficult to interpret, but the uniannulate condition is probably the most usual.

Just anterior to the jaws and separating them from the buccal area is a slight circular sulcus and fold. The jaws are low and rounded, not at all compressed on the free edge. As usual they may be retracted into little pockets so that the entire toothbearing surface is concealed. Each jaw bears a double file of large, coarse teeth arranged in from twelve to sixteen pairs. The pharynx reaches to X and has from nine to twelve or more longitudinal folds, three of which unite into a strong ridge behind each jaw. The long narrow stomach reaches to XIX, and is provided along its entire length with numerous small pockets; at its posterior end a pair of large cæca arise and reach caudad to XXII or XXIII. The intestine is also straight and bears two or three pairs of quite large, short, globular cæca which lie dorsad of the large posterior gastric cæca. The anus is very large.

The customary ten pairs of testes are present in the anterior end of somites XIV to XXIII each reaching into the preceding somite. The collecting portion of the vasa efferentia and vas deferens are essentially similar to those of *Macrobdella*. The epididymis is a rather narrow tube, much convoluted, rather open and not at all massive. The epididymis opens into the small fusiform sperm sac in the posterior part of XIII and the latter is continued as the ductus ejaculatorius. This canal reaches forward to the level of the male pore and then bends back to join the closed end of the atrium, sometimes the right, sometimes the left one, passing beneath the nerve cord. The atrium or penis sheath is very long and slender, with a sharp bend at ganglion XVII, from which point one limb reaches to the male pore, the other to the anterior end of somite XV; the ratio of the

short and long limb is about as one to two and one-third. The penis is a slender filiform organ with a slightly bulbous extremity and is frequently extruded to a length of three times the width of the leeches body. The male orifice is on the anterior part of XI *b6* or, less frequently, between this and the preceeding annulus.

The paired ovaries are situated in the posterior part of XIV dorsal of the nerve cord and in contact with the second pair of testes. There is a large albumen gland and a long narrow common oviduct which opens into the narrow anterior end of the pyriform ovisac lying in somite XVI. From the posterior end of the latter a long, slender, much convoluted vagina reaches to the female orifice at XII *b6* or XII *b5/b6*.

*Hæmopsis marmoratis* includes many color varieties. The ground is usually some shade of green, olive green or greenish brown, sometimes nearly plain, sometimes remotely spotted, but usually thickly and confluent blotched with irregular or intermixed spots of lighter grays and darker browns or black. The lighter kinds tend to predominate on the ventral side, from which the darker pigments may be altogether absent. The darker markings are sometimes so close on the dorsal surface as to produce an almost black color.

Habits—The horse leech, as this species is called, is found in practically all parts of North America, where it has a known wider range than any of its near allies. It is semi-aquatic, living in the mud by the sides of ponds, pools, and lakes rather than actually in the water, although it of course moves freely about in the water and is often found in the mud at the bottom. Along tidal rivers the species is most abundant beneath stones on the flats exposed at low water where it lives with several species of true earthworms. At times it wanders some distance away from the waters edge, burrowing in the soil in search of the earthworms on which it feeds; but it is not terrestrial in the sense in which *H. lateralis* is, never leaving, so far as has been observed, the near vicinity of water. Besides earthworms, various kinds of aquatic insects and their larvae, aquatic oligochaetes, gastropods and pelecypods are pursued and eaten and large quantities of mud containing organic matter are swallowed. The species is also, like many other leeches, a scavenger and great numbers will collect on the body of a recently killed animal thrown into their haunts. Blood is also taken when the opportunity is afforded of attaching itself to drinking cattle or the legs of boys wading in its haunts. It would be interesting to know if it ever enters the pharynx of cattle,

as is well known to be the habit of the *Limnatis* so common in some of the countries bordering on the Mediterranean.

***Hæmopsis lateralis* (Say) Moore.**

(Plate III, fig. 23)

*Hirudo lateralis* Say (1824).

? *Macrobdella valdiviana* et *gigas* Philippi (1872)

*Semicolex terrestris* Forbes (1890)

*Hæmopsis lateralis* Moore (1901)

Description—Although there are some minor differences I am unable to separate the aquatic leech originally described by Say from specimens procured in Minnesota from the interesting terrestrial form which Forbes has described and which was found by him in considerable numbers in garden soil in Illinois. So far only the aquatic variety has been found in Minnesota and was represented in the Survey collections by two living examples which unfortunately escaped from me and were lost.

Compared with the terrestrial variety, of which even Prof. Forbes' contracted alcoholic specimens reach a length of eight inches, a large number of the aquatic form, chiefly from Ohio and Maryland, average much smaller, about five inches long and one-half inch wide being the usual size. This species is much more slender than *H. marmoratis* and the greatest width lies farther caudad. The body is rather more muscular and as a consequence firmer, but during life exhibits the same variety of shapes and postures.

The mouth is somewhat smaller and the oral sucker narrower than is *H. marmoratis*, while a further slight distinction is found in the better developed longitudinal grooves beneath the lips of this species. The eyes have the same number and position as in the species last described.

In the few cases in which a clitellum has been observed it differs in no respect from *H. marmoratis*. Although not differing in any way from the typical arrangement in the family, the seventeen pairs of nephridiopores on the posterior margin of *b*<sub>2</sub> of somites VIII to XXIV inclusive are unusually distinct and lie just behind a sort of slight spout-like projection. The posterior sucker is noticeably small.

Throughout the entire length of the body the annulation is very distinct, and at the margins most of the annuli are rather sharply angulated. In most respects the somites are constituted just as in



*H. marmoratis* but the following features are diagnostic: Somite VII is fully quadriannulate and VIII quinquianulate, owing to the complete subdivision of VII  $a_3$  and VIII  $a_1$  each into two annuli; as a consequence this species has two more annuli in the anterior region; VI  $a_3$  and VII  $a_1$  are always relatively wider and may exhibit an incipient furrow; on the complete somites the annuli are not equal but bear the following relation:— $a_2 < b_1 = b_2 < b_5 = b_6$ , except at the posterior end of the series; finally XXVI and XXVII are typically biannulate.

Including the rudimentary denticles at the posterior end each jaw bears from twenty to twenty-five pairs of teeth, of smaller size and more irregular form than in *H. marmoratis*. In other respects the digestive organs are essentially similar in the two species.

The sperm sacs and epididymes do not reach beyond ganglion XI anteriorly, or ganglion XII posteriorly; the latter are massive and compact and partly envelope the sperm sacs to which they are closely moulded. The posterior bend of the atrium is at ganglion XIV and the relative length of the two limbs is as one to one and seven-tenths in three examples measured. Although the genital pores are in the homologous annulus they lie two annuli farther from the mouth than in *H. marmoratis*. The ovaries are always within somite XII, and the vagina never extends posterior to ganglion XIV.

Forbes thus describes the colors of living examples of the terrestrial variety—"sooty drab, varying to plumbeous black, somewhat lighter beneath, uniform in tint and quite without spots or mottlings of any sort. A darker median longitudinal stripe, very conspicuous and well defined, is almost invariably present; a paler marginal stripe often approaching buff, little less constantly so; and a ventral sub-marginal stripe of the same color as the median dorsal one likewise quite frequent." The ground color of the aquatic variety is similar, but while the dorsal black stripe is less constant it may be very conspicuous; more frequently it is faint and obscure, broken into small spots or totally wanting. A few small dark spots are sometimes scattered over the dorsum. Sensillæ are much more distinct in the aquatic than in the terrestrial variety; indeed Forbes failed to find them in the living specimens of the latter.

Habits—In habitat, food, movements, resting attitudes etc. the aquatic variety is essentially like *H. marmoratis*. It is capable of a greater degree of extension and appears to be a more active swimmer than that species. Two examples sent to me by Prof. Nachtrieb and

the only ones included in his collections were placed in an aquarium with *H. grandis*. One night the cover was accidentally left displaced and on my arrival the following morning both were gone, but none of the other species were missing. A shining track of dried mucous on the polished floor showed the course of their wanderings. One quickly disappeared beneath a wall case. The other was tracked for a measured distance of more than fifteen yards, when it too disappeared beneath the wash-board. Neither was recovered, but the circumstance is mentioned as showing the tendency of this species to wander and its ability to live in a perfectly dry situation, and as further confirmation of my opinion of the identity of this with the land leech of Illinois. Under the same circumstances *Hæmopsis marmoratis* or *Erpobdella punctata* would have quickly died before having crawled nearly so great a distance, as I know from experience. Concerning the terrestrial form Prof. Forbes writes of having obtained fifty-six specimens, all from the earth in central Illinois and some of them half a mile or more from the nearest water, while none occurred in the course of a large amount of aquatic work done in the same regions during the same period. Its only known food is earthworms which it swallows entire. From the fact that his specimens were all obtained from March to June, Prof. Forbes suggests that it is probable that this species penetrates the soil to considerable depths during the midsummer draughts. So far as I know the terrestrial form has been taken by no one else in this country, but a very large terrestrial leech found by Philippi in Chile is indistinguishable in the description and excellent figure from Forbes species.

*Hæmopsis plumbeus* sp. nov.

(Plate IV. figs. 29, 30, 31)

? *Hirudo lateralis* Say (1824) in part.

Description—Though resembling *H. lateralis* quite closely in color this hitherto unnamed form stands much nearer to *H. grandis*, to be next described, in respect to both internal and external structure. The features in which it differs from the latter are rather slight but have proved quite constant in all of the specimens examined. Probably this species does not equal *H. grandis* in size, the available specimens varying between two and six inches in length. The form is heavy like that species, and the oral sucker larger and lips much broader. A rather wider unsegmented rim borders the sucker. Except that they are rather larger the eyes are like those of *H. grandis* in structure and arrange-

ment. The sensillæ, nephridiopores and anus present no distinctive features. None of the specimens examined has the clitellum developed.

The annulation is essentially like that of *H. grandis* but a few differences occur, which may disappear when a larger series of specimens comes to be compared. The furrows are well marked but present little of that zigzag character and secondary wrinkling which is so conspicuous in the larger species. This difference is very marked in specimens of the two species of equal size and preserved together, so that it may prove not to be accidental. The furrow V *a1/a2* is quite incipient and the annuli VII *a3* and VIII *a1* are relatively much smaller and very much less distinctly subdivided than in *H. grandis*.

The mouth is very large and the ventral surface of the lip shows no trace of longitudinal sulci. Jaws are absent and the capacious pharynx bears twelve very low longitudinal folds. The remainder of the alimentary canal appears to differ in no way from that of *H. grandis*.

The external genital orifices are constantly in the middle of annuli XI *b6* and XII *b6* respectively, while in *H. grandis* the male pore is almost invariably at XI *b5/b6* and the female in the anterior part of XII *b6*. The penis is filiform and may protrude to a length of two and one-half times the width of the body at the male orifice. It is in the structure of the internal reproductive organs that the most evident differences between this species and *H. grandis* are found. In fact the resemblance is much closer to *H. marmoratis* in respect to these organs. The atrium extends caudad far beyond the vagina to the neighborhood of ganglion XVI where the usual sharp bend occurs. The short limb is about one-half as long as the long one. Relatively small sperm sacs, which are not more than one-fourth or one-fifth of the length of the atrium, lie far forward in the region of the male orifice. The coils of the epididymes lie chiefly by the side of the sperm sacs and not heaped up at their caudal end as in *H. grandis*. Unlike any other species of the genus described in this paper the vagina is very much shorter than the atrium, reaching only to the caudal end of the somite XIV. The common oviduct lies on the dorsal side of the vagina; the albumen gland is large and nearly spherical and the ovaries are just in advance of the female pore.

The color is a remarkably uniform leaden or slaty gray, usually purer and sometimes darker below, and often showing a slight olive or yellowish tinge above. Along the entire lateral margins from the

caudal sucker to the lips is a broad, dull but conspicuous rufous or orange band which broadens and encroaches on the dorsal surface as it approaches close to the head, but contracts again on the lip to a narrow marginal line. The ventral margin of this band is, owing to the purer ground color below, more sharply defined. Small irregular spots of black are scattered more or less remotely over the dorsum, being usually most numerous toward the margins and ends of the body, especially in the specimen figured. Sometimes they are almost absent and are never numerous. Except for a few along the lateral rufous band the ventral surface is free from spots. The caudal sucker is of the ground color both above and below, with a narrow rufous border.

Nothing distinctive concerning the habits of this leech is known to me and I have seen no examples except those in this collection from northern Minnesota.

It seems very probable that the presence of spots which Say attributes to his *H. lateralis* may have applied to this species rather than the one which is represented by Say's supposed type. The spots are much more conspicuous and constant in this than in that species and as the coloring is otherwise almost identical and both species occur in the precise region from which his types came Say might easily have confused them.

### ***Hæmopsis grandis* (Verrill).**

(Plate IV, figs. 26, 27, 28; Plate V, fig. 37)

*Semiscollex grandis* Verrill (1874).

Description—As Prof. Verrill indicated in his original description this is a monster among American leeches, exceeding the North American representatives of the terrestrial variety of *H. lateralis* and at least equaling the larger representatives of that species which Philippi has described from Chile under the names of *Macrobdella valdiviana* and *M. gigas*. Living examples not infrequently exceed a foot in length and specimens of fifteen or even eighteen inches have been reported from the lakes of Minnesota. However, this is an unusual size and smaller individuals having a length of from five to eight inches are much more common.

The body is very robust and heavy posteriorly, but rather slender anterior to the clitellum. While seldom much depressed the body does not assume the quite rounded form frequent in *H. marmoratis*, which some varieties of this leech closely resemble in general aspect. In

life the body is soft and limp and possesses a great facility for contraction and elongation and other changes of form.

While large, the mouth is more contracted than in *H. plumbeus* and the lip narrower and more prolonged. The five pairs of eyes have the arrangement usual in the family; they are all of relatively small size and the fourth and fifth pairs quite inconspicuous.

The clitellum is a thick and prominent glandular girdle extending over fifteen annuli from X *b*<sub>5</sub> to XIII *b*<sub>2</sub>, often rather within the latter but apparently never as far as its middle. The female orifice is similar but drawn out laterally to a slit-like form and usually well within annulus XII *b*<sub>5</sub>, sometimes as far back as its middle or so far forward as to lie in the furrow XII *a*<sub>2</sub>/*b*<sub>5</sub>.

Seventeen pairs of nephridiopores can be readily distinguished on the posterior margins of the first annulus (*a*<sub>1</sub>) of VIII and the second annulus (*b*<sub>2</sub>) of somites IX to XXIV inclusive. They, together with the metameric sensillæ, have the positions usual in the genus and the marginal sensillæ show the same tendency to become subdivided. There are no cutaneous papillæ, the skin being smooth. However, the short shallow wrinkles seen in many large leeches are remarkably conspicuous in preserved specimens of this species and give to the interannular furrows a peculiar zigzag course which is especially pronounced toward the ends of the body. The usual non-metameric sense organs are present in abundance and are especially numerous on the lips. The annulation differs in no essential feature from that already described for *Haemopsis marmoratis*.

While retaining all of the characteristics of the genus the reproductive organs differ considerably in the proportions of the several regions of the complicated ducts from all of the other species found in Minnesota. The epididymis is remarkably massive and lies chiefly caudad of the corresponding sperm sac which is consequently not so largely enclosed in its coils as in *H. lateralis*. The sperm sac is remarkably large, being much wider than and about half as long as the atrium when fully distended, as in the specimen figured. Its anterior end is just behind ganglion XII and tapers into the ductus ejaculatorius which is noteworthy for its shortness. In almost every instance the atrium is doubled on itself at about the middle, so that the two limbs are approximately equal and the blind glandular end is usually a little anterior to the male pore. Either the right or left ductus ejaculatorius may pass beneath the nerve cord.

The ovaries are situated in the anterior part of XIII immediately

behind the female pore, and both may lie dorsad of the nerve cord or one pass beneath it. There is a large pyriform albumen gland, a short common oviduct and a relatively short, thick vagina.

A median and one or two pairs of lateral longitudinal furrows, together with some less constant and minor ones, mark the ventral surface of the lip. The transverse sulcus dividing the buccal chamber from the pharynx is deeper than usual, which is perhaps correlated with the entire absence of dentigerous jaws in this as in the last described species. Although somewhat variable and irregular there are typically about twelve prominent longitudinal pharyngeal folds. Nine of these are in three groups of three each coalescing anteriorly at what would be the position of the jaws in other species. Three, unusually simple and frequently incomplete folds, alternate with these. The stomach scarcely shows any indication of lateral pouches and the posterior pair of cæca are remarkably short, scarcely one-half the length of the intestine.

On the dorsal surface the ground color varies from tawny olive through olive and olive green to oil green, the green colors being nearly pure in some examples, especially in those which are least spotted. In others they are impure from the suffusion of brown or dusky pigments in the deeper tissues, in extreme cases imparting to the entire dorsum a brownish hue. The lighter greens appear most frequently toward the anterior end and on the caudal sucker, but in many examples these regions become dusky. Frequently a marginal rufous or orange stripe is present, especially toward the posterior end, but it is seldom or never so clearly defined as in *H. plumbeus*. The ventral surface is gray, yellowish or light brown but always paler than the dorsum.

There is a great range in the degree of maculation which, as compared with *H. marmoratis*, is characterized by a greater boldness and distinctness in this species. Perhaps the most typical condition is that in which the dorsum of each complete somite is marked by eight or ten irregular but somewhat quadrate black spots, most of which are confined to the limits of one annulus, but a few, especially toward the margins, are larger and more irregular. In other cases the spots are much more numerous and confluent so that the real ground color appears as lighter areas on the dark field. Still others are as nearly free from spots as some examples of *H. plumbeus*. The ventral surface bears fewer spots than the dorsal and not infrequently is quite immaculate.

**Habits**—This great leech is found on the shores of the Great Lakes and abounds in the numerous lakes and ponds of Wisconsin, Minnesota and Michigan. Eastwardly it extends its range through New York into New England but is rare in the Middle States and I have had but little opportunity to study its habits under natural conditions.

It appears to live chiefly about the borders of the bodies of water which it affects, concealing itself beneath stones. According to Barrows it secretes an unusual abundance of mucous and I suspect from this fact and the large size of the nephridial bladders that it may upon occasion leave the water. Stomach examinations show that its food consists of earthworms and allied aquatic worms, smaller leeches, particularly the nephelids, snails, insect larvæ and organic mud. In captivity several individuals fed voraciously on earthworms but could not be induced to attack fishes, frogs or turtles even when the skin was abraded so that the blood flowed, from which behavior it would appear that the accounts of this species habitually attacking fish require to be verified.

#### **Family Herpobdellidæ.**

Leeches of mostly moderate size and slender elongated form, usually terete anteriorly, often much depressed posteriorly. Clitellum as in *Hirudinidæ*. Oral sucker small, forming lips; caudal sucker also small, discoid. Complete somites fundamentally of five rings, but one or more often subdivided, forming six to eleven rings. Eyes usually four pairs, two pairs on somite II often coalesced, two pairs of smaller size on IV; but sometimes eyeless. Cutaneous sense organs and papillæ numerous, not obviously metameric. Mouth and pharynx as in *Hirudinidæ*, but the latter with three longitudinal muscular ridges and no jaws. Stomach and intestine straight, simple and without diverticula. Genital orifices variable in position, the male usually on XII, the female on XIII. Testes sacs small and very numerous, extending through about segments XVIII to XXIII. Sperm ducts very long and much convoluted, paired until they empty by means of the short prostate cornua into the small median atrium. No protrusible penis. Ovisacs long and slender as in *Glossiphonidæ* but each doubled on itself, united only at the external orifice. Copulation takes place and spermatophores are implanted on the integument. Eggs enclosed in flat, pouch-like chitinous cocoons fastened by one side to stones, sticks, plants, etc. Fresh water predaceous leeches, feeding on insect larvæ, worms, etc., occasionally suck the blood of vertebrates.

**Genus *Erpobdella* Blainville.**

Size moderate; posterior region not greatly depressed. Spermiduct forming a long loop (reaching to ganglion XI) anterior to atrium, which is provided with a pair of simply curved horns. None of the five annuli of complete segments distinctly enlarged and subdivided.

***Erpobdella punctata* (Leidy) Moore.**

(Plate IV. fig. 39)

*Nephelis punctata* Leidy (1870)

*Nephelis lateralis* Bristol (1898) in part.

*Erpobdella punctata* Moore (1901)

Description—The form is elongated with the sides nearly parallel, tapering anteriorly to the clitellum but very little at the posterior end. Anteriorly it becomes almost circular in section and posteriorly, although margins are sharp and prominent, is little depressed and widened. The size is large for the family, reaching a length of about five inches. The body is very firm, hard and muscular.

The oral sucker is very small, being little more than a short lip overhanging the nearly terminal mouth. Normally there are three pairs of eyes, the first decidedly the largest and situated close together on somite II and directed forward; the others more widely separated on the sides of IV and looking somewhat backward. The clitellum is frequently seen in full development, in which condition it is a wide, thick complete girdle covering the fifteen annuli from X *b*<sub>5</sub> to XIII *a*<sub>2</sub> inclusive. The male pore is a rather conspicuous opening at XII *b*<sub>2</sub>/*a*<sub>2</sub>, the female a much smaller one at XII *b*<sub>5</sub>/*b*<sub>6</sub> or two annuli farther caudad.

Somites I, II and III are uniannulate; IV and V are biannulate, VI is triannulate, VII quadriannulate; and VIII to XXIV inclusive, or seventeen somites, are quinquannulate. At the posterior end somite XXV is quadriannulate, though the last annulus (*a*<sub>3</sub>) may be more or less distinctly subdivided on the dorsum; XXVI is either biannulate or triannulate and XXVII is usually uniannulate.

In the complete somites the annuli are of approximately equal length and *b*<sub>6</sub> is not obviously enlarged or more completely subdivided than the others. Numerous small cutaneous papillæ bearing sense organs appear arranged in an irregular transverse row on each annulus. They are largest dorsally and on the neural annulus. The annuli of the simpler somites frequently exhibit two such rows, indicating their composite character.



The testes are numerous, about fifty to sixty on each side of somites XVIII to XXIV, mostly with separate vasa efferentia. The enlarged and much convoluted epididymis or sperm sac reaches from XVIII to XIV. There is a long pre-atrial loop to the ejaculatory duct reaching to ganglion XI. The atrium consists of a small eversible bursa and a pair of elongated semi-erect, curved prostate cornua, the bases of which are enveloped by a thick layer of prostate glands. The ovaries are elongated sacs each doubled on itself and reaching for a variable distance through the ventral sinus.

In this species the color varies extremely. Young individuals usually contain little or no pigment, permitting the red color of the blood to appear through the translucent tissues. The adult pigmentation is assumed gradually with increase in age and size. When full grown the ground color may be plumbeous, slate color, brownish gray, olive brown, fuscous, light brown or chocolate, always somewhat lighter ventrally and in the furrows and enlivened on the margins by the red tint of the lateral blood vessel. Sometimes a beautiful golden green hue overspreads the entire dorsum. The browns are most usual and may be plain or more usually more or less marked with irregular black spots with light centers, arranged in two or four longitudinal lines leaving the middle of the back and the margins clear.

Habits—Within the area of its distribution, which is extensive, this leech occurs under a great variety of conditions. Almost every spring, brook and river, ditch, pond and lake, no matter how pure and cold or how warm and foul, is its home. And in most situations it is by far the most common species of leech present, exceeding in numbers even the omnipresent *Glossiphonia stagnalis*. The size varies greatly with the extent of the body of water and the richness of the food supply. Small clear brooks and ditches almost invariably yield only small individuals, while by far the largest individuals which I have seen come from large rivers and ponds and the Great Lakes. Bristol has pointed out that in any particular pond they congregate on the shore which receives the richest food supply and my own experience substantiates this.

Like many other species of leeches this one conceals itself during the day beneath stones, logs, leaves or whatever happens to be convenient for the purpose, but leaves its shelter at night and searches actively for food. In aquaria the rhythmic respiratory movement, which takes place while either both or only the posterior sucker is attached, may be frequently observed. It is so muscular and the body so

hard, wiry and slippery that it is really quite difficult to hold a living one between the fingers. When picked up it struggles and writhes violently and when disturbed creeps rapidly. It is also the most expert and active swimmer of any of our common leeches. When swimming it turns edgewise and undulates the body in eel-like fashion, sometimes elevating the head above the surface.

Although somewhat of a scavenger, it subsists chiefly on aquatic insects and their larvæ, and aquatic oligochaetes, but will attack fishes and frogs or draw blood from the legs of wading boys. Not infrequently cannibalistic tendencies appear, large individuals devouring the smaller ones of their own species. It is very active in seeking food and will pursue its prey with considerable tenacity.

Breeding continues over a long period—most of the spring and summer. Spermatophores are formed and attached to any part of the body except the anterior end which seems to be avoided. In copulation the two leeches wind about each other and adhere by means of their suckers and the exchange of spermatophores may be mutual. The small, flat, amber-colored egg cases are familiar objects to students of fresh water life and are often found in great numbers attached to the underside of stones etc. in the water.

### Genus *Nephelopsis* Verrill.

Size large; much depressed posteriorly. Sperm duct forms a loop as in *Erpobdella*; atrial cornua prominent and with a complete spiral turn. All annuli of complete somites more or less distinctly subdivided.

### *Nephelopsis obscura* Verrill.

(Plate V. figs. 35, 36; Plate VI. fig. 40)

*Nephelopsis obscura* Verrill (1872).

Description—Like the species last described this is a rather large leech, attaining a length nearly equal to *Erpobdella punctata* and considerably exceeding it in the breadth of the posterior region of the body. Compared with other species of the family belonging to the Minnesota fauna the body is more depressed and in its posterior part very much broader than they. The margins are sharp and prominent. The region anterior to the clitellum is relatively slender and sub-depressed with rounded margins. Texture hard and firm.

Nothing characteristic appears in connection with the mouth and lip which is rather broad. There are four pairs of eyes of about equal

size; the anterior two pairs are situated nearly side by side in somite II, or the more lateral pair in a slightly more caudal position on the furrow II/III. Both are directed forward and slightly lateral. The remaining two pairs are situated farther back but similarly close together on the sides of the oral annulus IV. Usually they are on the posterior part of the larger annulus but their pigment cups may lie beneath the furrow  $a_2/a_3$ . Both are directed caudad and laterad.

Fifteen annuli, X  $b_5$  to XIII  $a_2$  inclusive, are occupied by the prominent clitellum. The external genital orifices are separated by two annuli situated as in *E. punctata* at the furrows XII  $b_2/a_2$  and XII  $b_5/b_6$  respectively. In individuals which are in active sexual condition, the male orifice is a conspicuous opening more or less elevated on pouted lips marked by radiating furrows. Occasionally the genital bursa is everted as an elliptical disc with a central platform-like elevation perforated by a single median pore or a pair of pores, dependent on the more or less complete protrusion of the organ. In small individuals and those not sexually active the male pore is minute, as the female invariably is.

The anus is a rather large transverse slit with wrinkled margins situated in XXVI and succeeded by several rather ill defined annuli belonging to XXVII. The caudal sucker is a thin, flat, expansive and largely exposed disc. Its dorsal surface is marked as in *E. punctata* by six or eight radiating ridges.

In one respect the reproductive organs are very characteristic. While in general resembling *E. punctata* the atrial cornua are larger and coiled in a complete spiral turn, which is invariably present in a large number of individuals of all sizes and conditions which have been dissected. The pre-atrial loops reach to ganglion XI.

The ground color is generally gray, clay color or brownish, the latter occurring most frequently on plain unspotted examples. By far the greater number of specimens are thickly spotted over the entire dorsal surface with black. These blotches are not coarse and heavy as in *Hæmopsis marmoratis* to which the species exhibits some resemblance in color, but are finely branched and ramifying, with frequently anastomosed terminal branches, thus affecting a more or less evident and continuous network. Sometimes the black spots are quite few and remote, again they become so predominant that the ground color is very largely obliterated and the dorsum presents a generally slate black color spotted more or less remotely with the lighter ground.

In any case, whether the spots be few or many, there is no evident

metamerism in its pattern and no tendency toward the formation of longitudinal stripes, the pigment being quite as continuous across the middle line as elsewhere. Except in the very heavily blotched specimens, in which a few spots occur, especially toward the margins, the ventral surface is immaculate.

Habits—The exact geographical range of this species is not yet known but it is especially characteristic of the Mississippi Valley and the lake region drained by the headwaters and tributaries of that river. It is exceedingly abundant in Wyoming, Wisconsin and Minnesota, but is known to extend as far south as Alabama. The stomachs contain large numbers of insect larvæ, which appear to furnish the chief sustenance, but also various species of Oligochæta, aquatic snails etc. No opportunity has been afforded me to study the habits of this species but there is no reason to believe that they differ materially from those of *E. punctata*. Verrill has described the egg cases as "broad oval or elliptical, terminating in a point or mucro at each end, flat below, smooth and slightly convex above, with a thin margin. They were 5.5 mm. to 8 mm. long by 3.5 mm. to 4 mm. broad."

#### Genus *Dina* R. Blanchard.

Size rather small; not greatly depressed posteriorly. Sperm duct not forming a long anterior loop reaching to ganglion XI; atrial cornua small. Last annulus of each complete somite obviously enlarged and subdivided.

#### *Dina parva*. sp. nov.

(Plate V. figs. 33, 34; Plate VI, figs. 41, 43.)

Description—A number of small and imperfectly preserved leeches from Gull Lake show characters which readily distinguish them from any species of *Dina* previously described. The species exhibits certain resemblances to *Nephelis fervida* Verrill, and may indeed prove to be that species instead of the one which was so identified in my paper on the leeches of Illinois. There is nothing in the original description of *N. fervida* except the size which will permit one to discriminate between the two.

None of the specimens at hand exceed an inch in length in the partly contracted state and if alive and extended would not be more than one and one-half inches. Posteriorly the body is relatively wide and flat but anteriorly becomes nearly circular behind the mouth. The mouth and lips have the customary form. Unlike most of our Amer-

ican species there are four pairs of conspicuous black eyes, though variations in which one or both of the anterior lateral ones are absent occur in about ten per cent of those studied. The anterior eyes are larger than the posterior, those of the two pairs almost in contact and their pigment cups situated well within somite III. The posterior eyes are smaller, looking outwards and backwards from the lateral faces of the posterior part of IV.

The genital orifices are separated by a greater distance (normally three and one-half annuli) than is the case in any other known American species. The male pore is a conspicuous transverse opening elevated on a broad low papilla in the middle of XII *a2*, and the female a very minute opening between the annuli XIII *b1/b2*. Considerable variation, in the posterior direction, occurs in the position of the male pore. In about five per cent of the cases it has been found at the posterior part of its annulus, in the succeeding furrow (XII *a2/b5*) or even within the annulus XII *b5*. No variations in the position of the female opening have been observed. Nothing of importance can be noted with regard to the nephridiopores, anus or posterior sucker.

Concerning the annulation reference may be made to figures 33 and 34 on Plate V and figure 43 on Plate VI. Both somites II and III appear to be biannulate and at least the outermost pair of eyes of the anterior group are well within the latter. Somite V is also biannulate, VI triannulate and VII quadriannulate. Beginning with VII annulus *b6* shows its larger size and by IX is fully subdivided. In most of the complete quinquannulate somites, of which there are seventeen (VIII to XXIV), this large size of *b6* and its subdivision is very clearly manifested. Toward the caudal end XXV is quadriannulate, XXVI triannulate and XXVII two or three small rings behind the anus.

Owing to maceration the characters of the testes cannot be satisfactorily determined but apparently they are even smaller and more numerous than usual in the family. The specialized anterior portion of the vasa deferentia extends through a smaller number of somites than usual, the sperm sac reaching from ganglion XVI only to XIV or thereabout, within which region it is of large size and much folded. The pre-atrial loop of the ejaculatory canal reaches to ganglion XI and just before entering the atrial cornua the duct is folded laterally several times. The atrium itself has simply curved horns. Its median part crowds the twelfth ganglion somewhat caudad out of its usual position.

Whatever pigment may have been present has faded out completely in the preserved material. Nothing is known concerning the habits of this species.

***Dina fervida* (Verrill) Moore.**

(Plate VI, fig. 42)

*Nephelis fervida* Verrill (1874).

*Dina fervida* Moore (1901)

Description—The length of this species is not known to exceed three inches and more often reaches but two. The body is depressed posteriorly but rounded anteriorly. The mouth is of relatively large size and the lips broadly rounded. More characteristic is the large size of the caudal sucker which has a greater expanse than in most small nephelids, the anterior margin being more widely free and reaching as far forward as XXV *a2*. If one may judge from the preparations the body is not of particularly firm consistency; certain it is that the muscular system is less well developed than in the hard species. The usual thick prominent clitellum reaches from X *b5* to XIII *a2* covering fifteen annuli. The external genital orifices are separated by two annuli, the male being situated at XII *b2/a2*, the female at XII *b5/b6*. Three pairs of eyes are more usual than four. They resemble those of *E. punctata* except that the pigment cups of the first pair lie chiefly within somite III.

There is little of diagnostic value in the annulation. Some features of the sense organs are peculiar but have no considerable value in defining species. The last annulus (*b6*) of each somite is much longer and more fully and constantly subdivided than any of the others, as in other members of the genus.

The species is very readily distinguished from *D. parva* by the character of the reproductive organs. The testes occupy the lateral portions of somites XVIII to XXIV, and average in the one individual in which they were all counted thirty-two on each side of a somite. The several regions of the sperm ducts exhibit no peculiarities until the atrium is reached. Here the entire absence of a pre-atrial loop is noted, the ejaculatory canals stopping abruptly at the apices of the atrial cornua into which they enter. When the copulatory organ is fully retracted the ducti form no loop whatever anterior to the atrium but when, in protrusion, the cornua are drawn somewhat caudad, they sweep somewhat anterior to it in a broad curve. The atrium itself is characterized by the relatively large size and quite un-

divided form of the median portion and the widely divergent short cornua. In these respects and also in the fact that the prostate gland covers the dorsum of the median chamber as well as the bases of the cornua, this species resembles *D. microstoma* most closely.

Two distinct color varieties occur, both of which have a dusky red color, during life, due to the blood. In one, pigment appears to be nearly or quite absent, a condition which characterizes all of the young and a few of the adults. The other and more usual variety has the dorsum marked with more or less numerous minute black flecks which vary greatly in number and somewhat in arrangement. Many specimens are so little pigmented as to appear quite light colored; such are usually marked with a pair of dark longitudinal stripes one on each side of a clear median area, in others these stripes become very broad and in still others the whole dorsum except the margins is deeply pigmented.

Habits—So far as now known *Dina fervida* belongs to the fauna of the Great Lakes and the immediately surrounding region, where it is quite common. The food contents of the stomach consist largely of tubificid worms and some insect larvæ. Verrill has described the egg capsules which are attached to the leaves of Nuphar as "broad-oval or elliptical, above smooth and convex, translucent yellowish brown, with a thin, flat lighter border, each end prolonged into a short tubular neck, with a terminal orifice. Lower surface flat." They measure from 9.5 to 11.5 mm. long which seems remarkably large for a species of the size of this.

**PLATES I-VI  
AND  
EXPLANATIONS**

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**PART III**





## GENERAL EXPLANATIONS

Roman numerals I to XXXIV refer to somites.

The letters *a*, *b*, *c* and *d* with Arabic numerals refer to the annuli.

For a full explanation see pages 17 to 19.

The cutaneous papillæ are designated as follows:

|          |                |
|----------|----------------|
| dlp..... | dorso-lateral  |
| dmp..... | dorso-marginal |
| mdp..... | dorso-median   |
| mp.....  | median         |
| smp..... | supra-marginal |

The metameric sensillæ are designated as follows:—

|          |                 |
|----------|-----------------|
| dl.....  | dorso-lateral   |
| dm.....  | dorso-marginal  |
| md.....  | dorso-median    |
| sbm..... | sub-marginal    |
| sm.....  | supra-marginal  |
| vl.....  | ventro-marginal |
| vm.....  | ventro-median   |

♂ ..... Male, or the external opening of the male genital organs  
or its position.

♀ ..... Female, or the external opening of the female genital  
organs or its position.

Special legends will be found in the explanations of the respective  
plates.

## PLATE I.

### *Glossiphonia stagnalis*. x 20.

- Fig. 1. Dorsal view of the first twelve somites. The positions of the genital pores on the ventral side are also indicated.  
ng. .... nuchal gland.

### *Glossiphonia nepheloidea*. x 56.

- Fig. 2. Dorsal view of the first ten somites.

### *Glossiphonia fusca*. x 30.

- Fig. 3. Dorsal view of the first ten somites of a young example, showing the metameric sensillæ and papillæ.

### *Glossiphonia complanata*. x 18.

- Fig. 4. Dorsal view of the first ten somites. The paramedian stripes are shown but the papillæ and sensillæ are omitted.

### *Placobdella montifera*. x 13.

- Fig. 5. Outlines of part of the reproductive organs, dissected. The folds of the epididymis and ejaculatory canal are drawn aside to show their length. A portion of the ventral nerve cord is included to show the segmental position of the parts.

at. .... Atrium

de. .... Ejaculatory canal of the spermduct

ep. .... Epididymis

ov. .... Ovary or ovarian sac

ti. .... First testis

vd. .... Vas deferens

### *Placobdella rugosa*. x 5.

- Fig. 6. Dorsal view of the first ten somites. All of the papillæ and most of the metameric sensillæ are shown but not the color pattern.

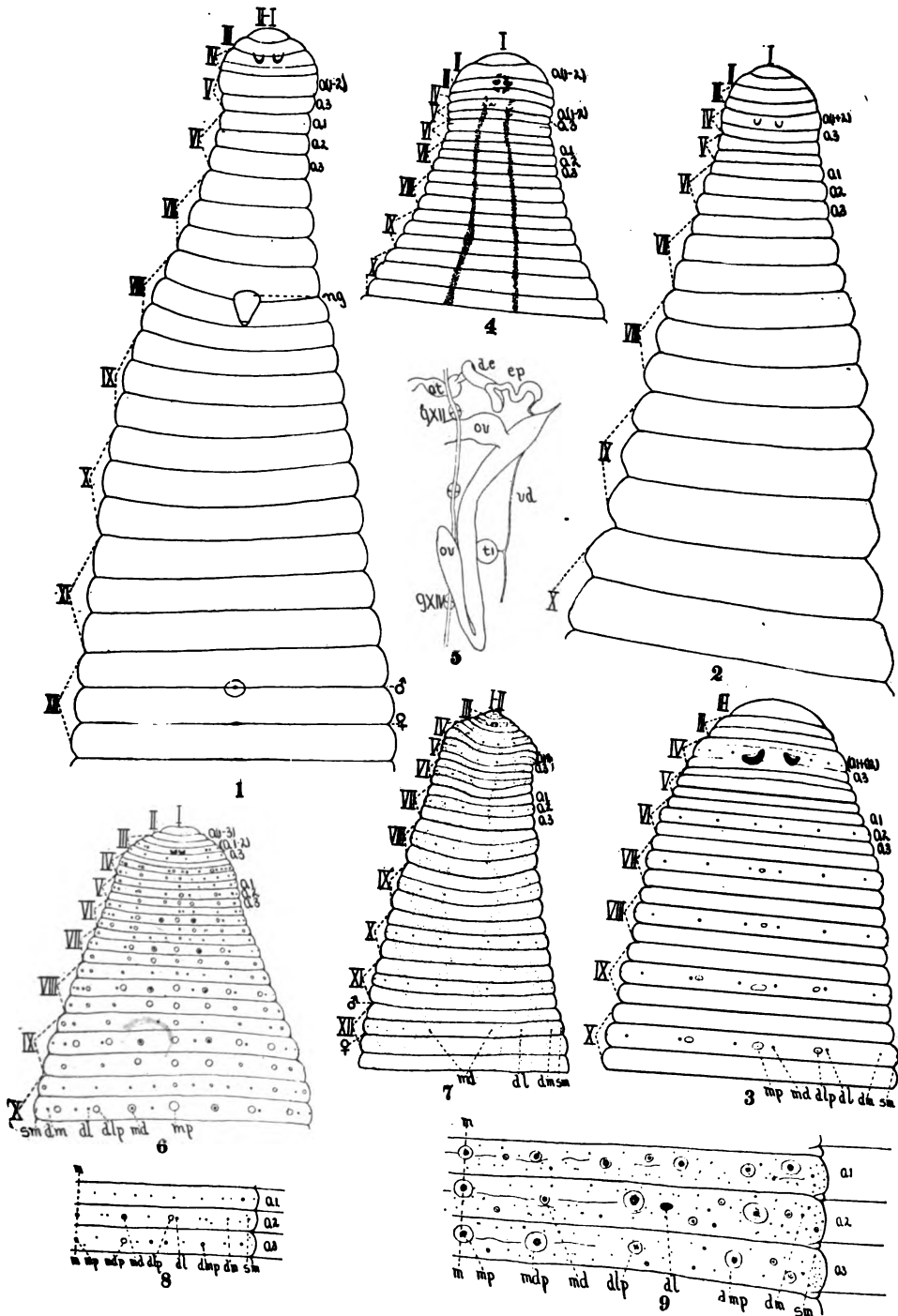
### *Placobdella parasitica*. x 5.

- Fig. 7. Dorsal view of the first twelve somites. The dark colored background is shown by stippling, the yellow vitta and spot being plain. The papillæ are omitted but the positions of the genital orifices on the ventral side are indicated.

- Fig. 8. Papillæ and sensillæ of the right half of the dorsal surface of somite XIX of a medium-sized example. The lines to the right indicate the relative positions of the furrows on the ventral side.

### *Placobdella rugosa*. x 5.

- Fig. 9. Papillæ and sensillæ of the dorsal surface of the right half of somite XIX of a large example. The lines to the right indicate the relative positions of the furrows on the ventral side.



## PLATE II.

### ***Placobdella montifera*. x 4.5.**

Fig. 10. The principal features of the external morphology of the dorsum of somites I-XII. Very slightly diagrammatic.

### ***Placobdella hollensis*. x 8.**

Fig. 11. Dorsal view of the first ten somites.

### ***Hemiclepsis occidentalis*. x 56.**

Fig. 12. Dorsal view of the first ten somites of a young example still remaining with the parent, showing the annuli and the eyes.

### ***Placobdella pediculata*. x 3.5.**

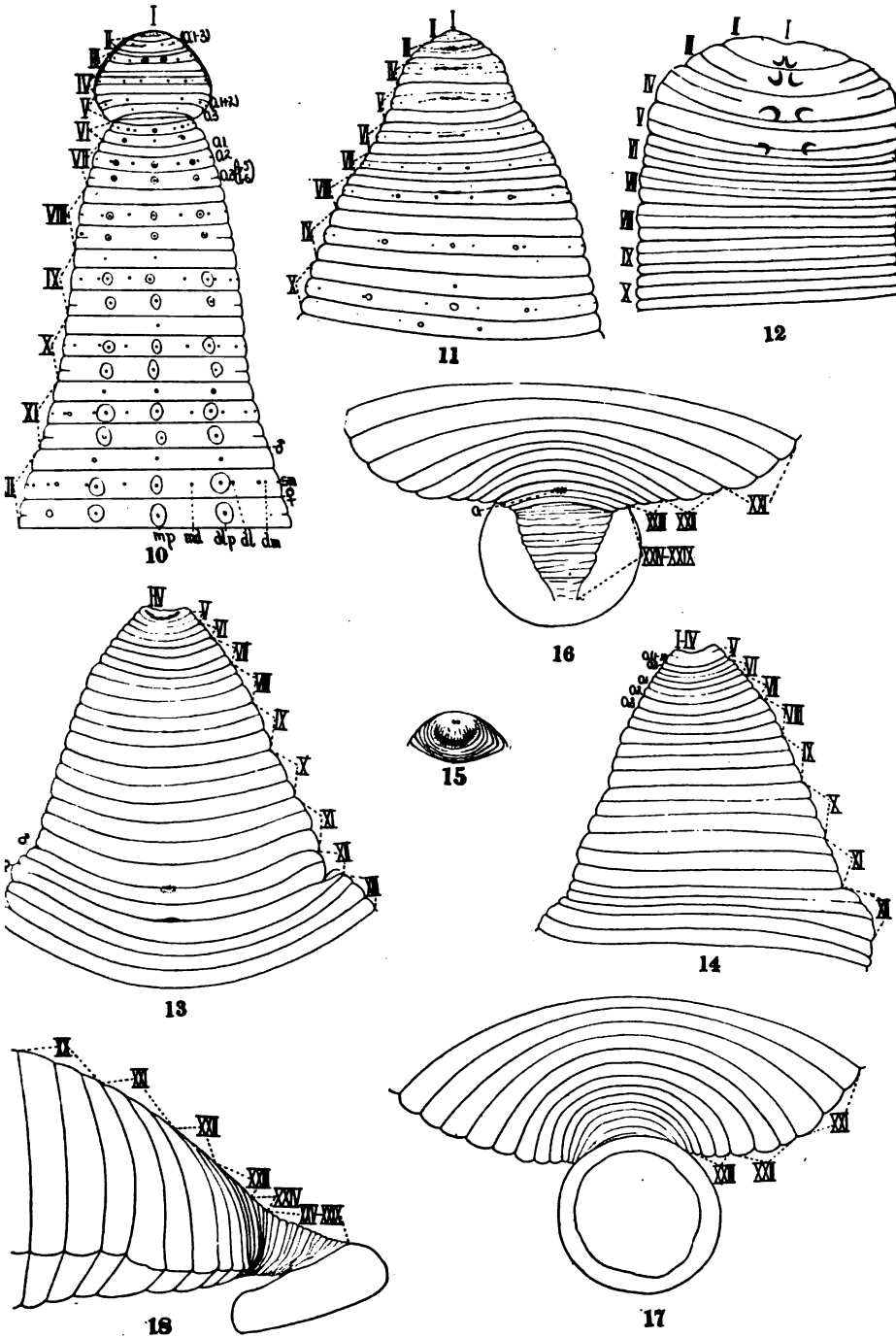
Fig. 13. Ventral view of the anterior thirteen somites.

Fig. 14. Dorsal view of the anterior thirteen somites.

Fig. 15. The head end as seen from in front.

Figs. 16, 17 and 18. Dorsal, ventral and lateral view respectively of the posterior end, showing the annulation and the peculiarities of the caudal sucker and its peduncle.

Plate II



Placobdella. Hemicleipsis.

### PLATE III.

#### *Actinobdella inequiannulata.*

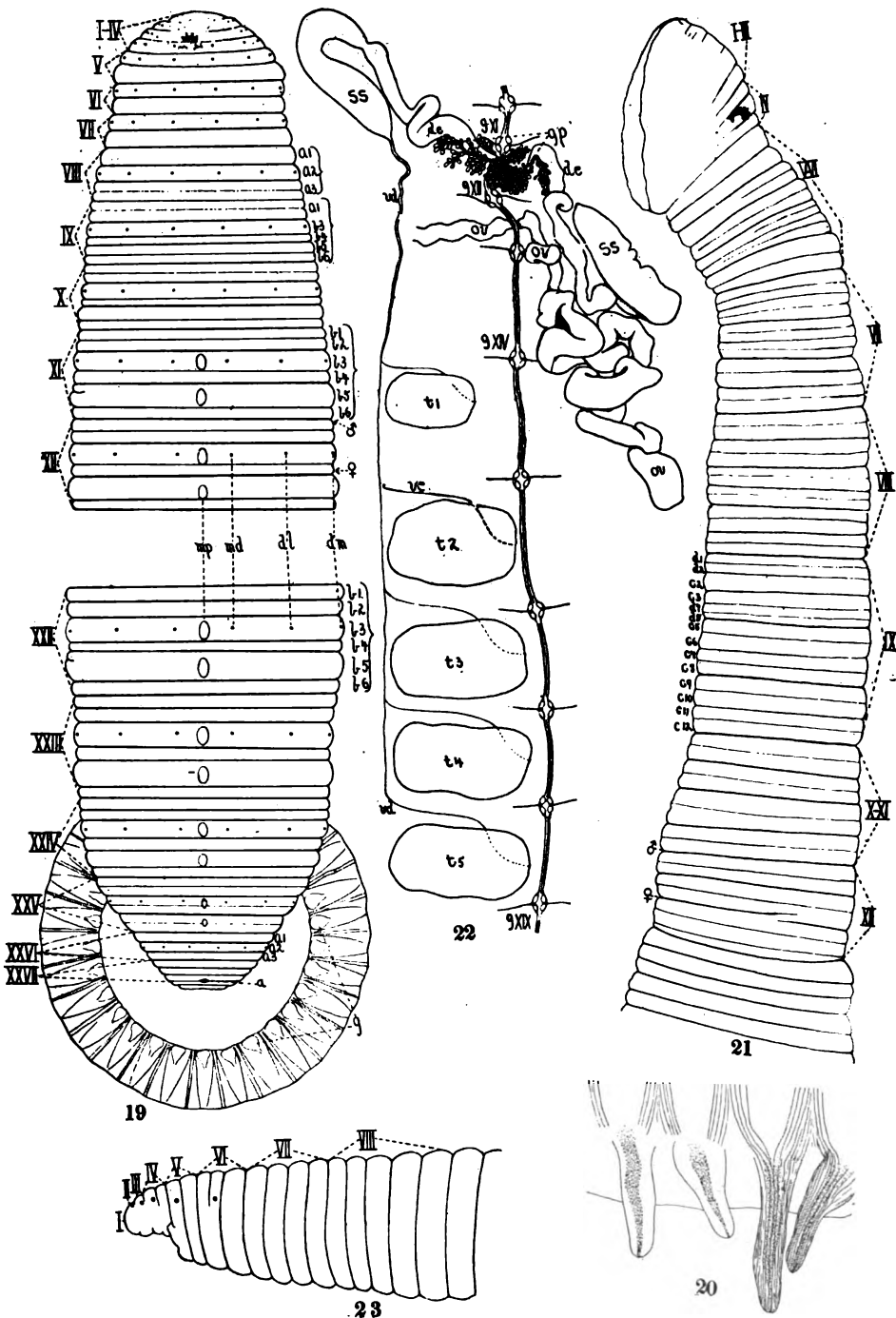
- Fig. 19. The external morphology of the dorsal surface. Somites XIII-XXI are omitted as they are precisely similar to those immediately preceding and following them. The furrows are drawn more regularly than they are in nature. x 35.
- Fig. 20. A small portion of the margin of the caudal sucker, viewed from within, showing four of the papillæ. The gland ducts are stippled and the muscles are represented by lines. x 130.

#### *Piscicola punctata.*

- Fig. 21. The first twelve and one half somites seen from the left side, showing the annulation as it appears in a well extended example. The limits of the somites anterior to VII and of X and XI are open to some doubt. x 35.
- Fig. 22. The dissected reproductive organs seen from the dorsal side. The testes of the right side and the ovary of the left side are omitted. The left spermduct is drawn forward to display its parts more fully.
- de. .... Ejaculatory canal of the spermduct.
  - gp. .... Prostate gland.
  - ov. .... Ovary.
  - ss. .... Sperm sac.
  - vd. .... Vas deferens
  - ve. .... Vas efferens
  - tl-t5 .... Testes of the left side

#### *Hæmopsis lateralis.* x 5.

- Fig. 23. Lateral view of the first eight somites, showing the annulation and eyes of the left side.



**Actinobdella. Piscicola. Hæmopis.**



PLATE IV.

**Macrobdella decora.** x 5.

Fig. 24. Dorsal view of the anterior nine somites showing the annulation, sensillæ and metameric color features. The lightly stippled blotches are red and the heavily stippled ones are black.

Fig. 25. Dorsal view of the posterior four trunk somites and sucker.

**Hæmopsis grandis.**

Fig. 26. Dorsal view of the anterior eight somites. X 5.

Fig. 27. Ventral view of the anterior eight somites. X 5.

Fig. 28. Dorsal view of several posterior somites. X 3.

**Hæmopsis plumbeus.** x 3.3.

Fig. 29. Dorsal view of the anterior eight somites, showing metameric sensillæ and black blotches.

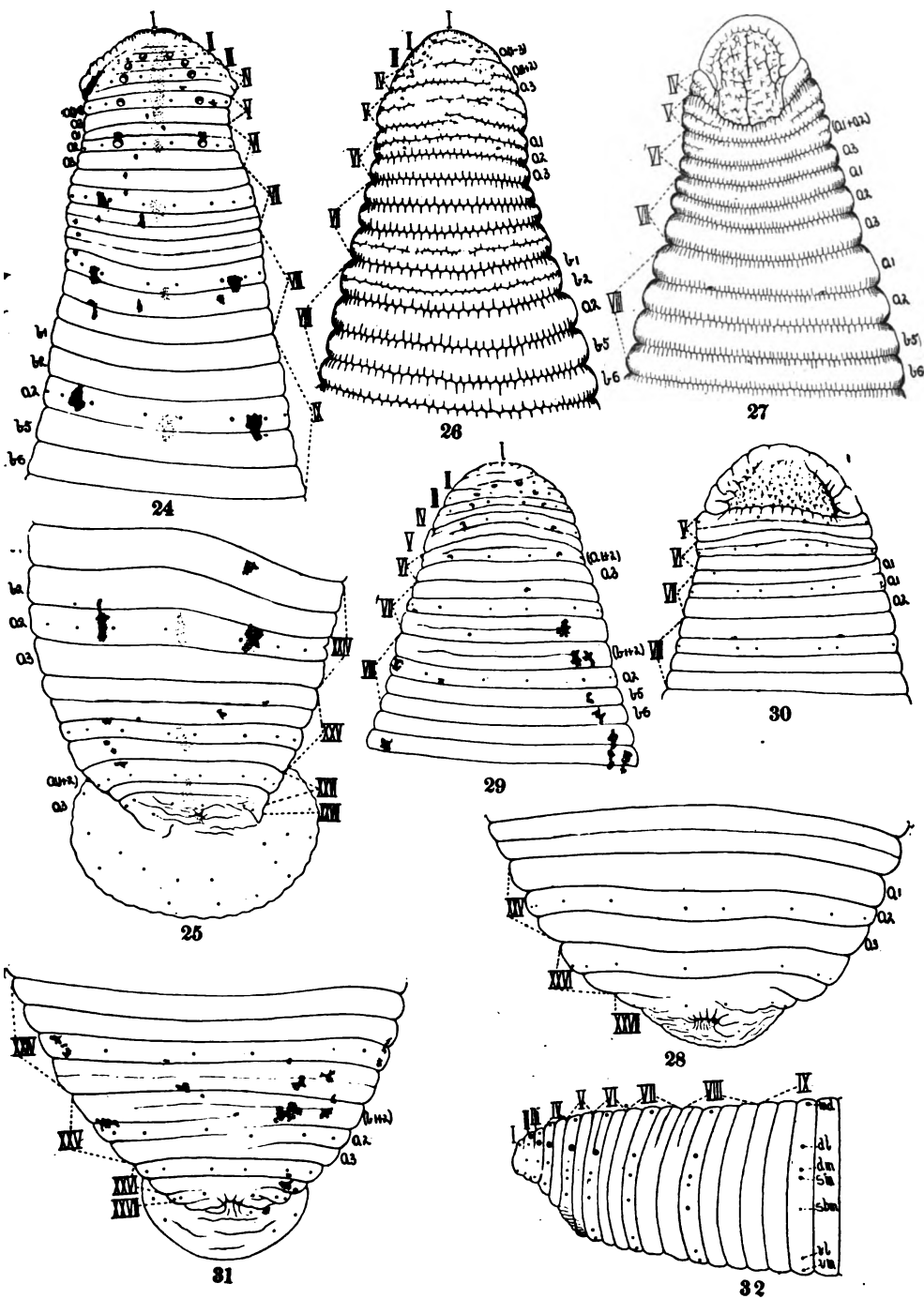
Fig. 30. Ventral view of the anterior eight somites.

Fig. 31. Dorsal view of several of the posterior somites.

**Hæmopsis marmoratus.** x 5.

Fig. 32. Lateral view of the anterior end, showing the annulation and metameric sensillæ.

## Plate IV



**Macrobdella. Hæmopis.**

PLATE V.

**Dina parva.** x 22.5.

Fig. 33. Dorsal view of the first nine somites, showing the annulation.

Fig. 34. Dorsal view of several posterior somites, showing the annulation.

**Nephelopsis obscura.** x 5.

Fig. 35. Dorsal view of the first nine somites, showing the annulation.

Fig. 36. Ventral view of the first nine somites.

**Hæmopsis grandis.** x 3.

Fig. 37. Dorsal view of the characteristic portions of the reproductive organs dissected out. The right sperm sac and the epididymis have been somewhat displaced to better expose the vagina &c.

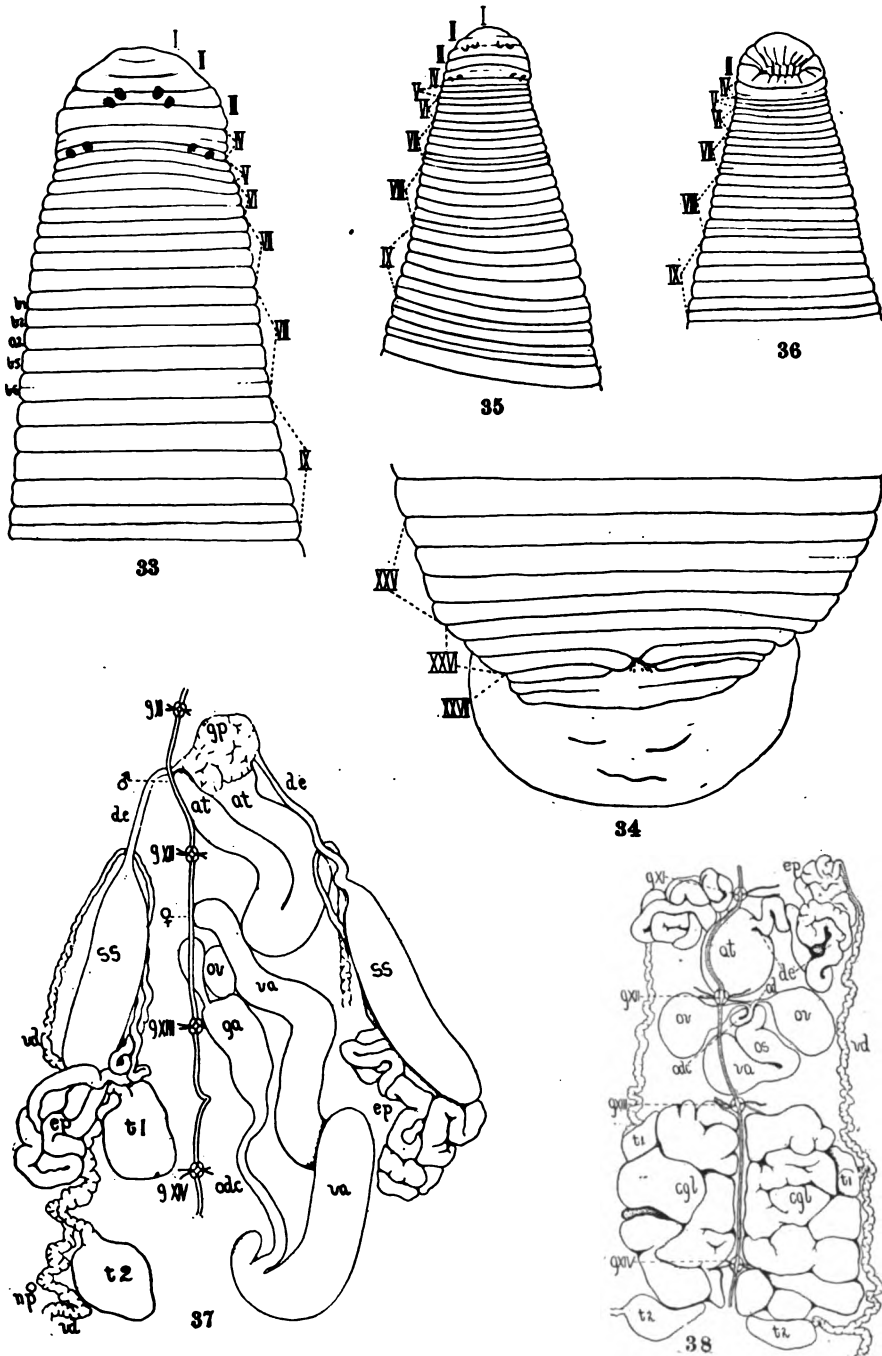
at.....Atrium  
de.....Ejaculatory canal of the spermduct  
ga.....Albumen gland  
gp.....Prostate gland  
odc.....Common oviduct  
ov.....Ovary  
ss.....Sperm sac  
tl, t2.....Testes  
va.....Vagina  
vd.....Vas deferens

**Macrobdella decora.** x 4.

Fig. 38. Dorsal view of the reproductive organs somewhat dissected out.

cgl.....Copulatory glands  
od.....Oviduct  
os.....Egg sac  
Other letters as for figure 37.

## Plate V



**Dina. Nephelopsis. Hæmopis. Macrobdella.**

## PLATE VI.

at .....Atrium  
de.....Ejaculatory canal of the spermduct  
of.....Closed end of ovarian sac  
ov.....Ovary or ovarian sac  
p.....Right prostate horn of the atrium  
ss.....Sperm sac  
t .....Testis or testes sac  
vd.....Vas deferens  
♀ .....female genital orifice

### *Erpobdella punctata.* x 7.5.

Fig. 39. Dorsal view of the dissected reproductive organs. All the testes, the spermduct on the right side and the ovary on the left side have been omitted.

### *Nephelopsis obscura.* x 5.

Fig. 40. Dorsal view of the reproductive organs. Only about one half of the testes of the left side of somite XVIII is shown. The ovary of the left side and all of the testes and most of the vas deferens of the right side have been omitted.

### *Dina parva.* x 10.5.

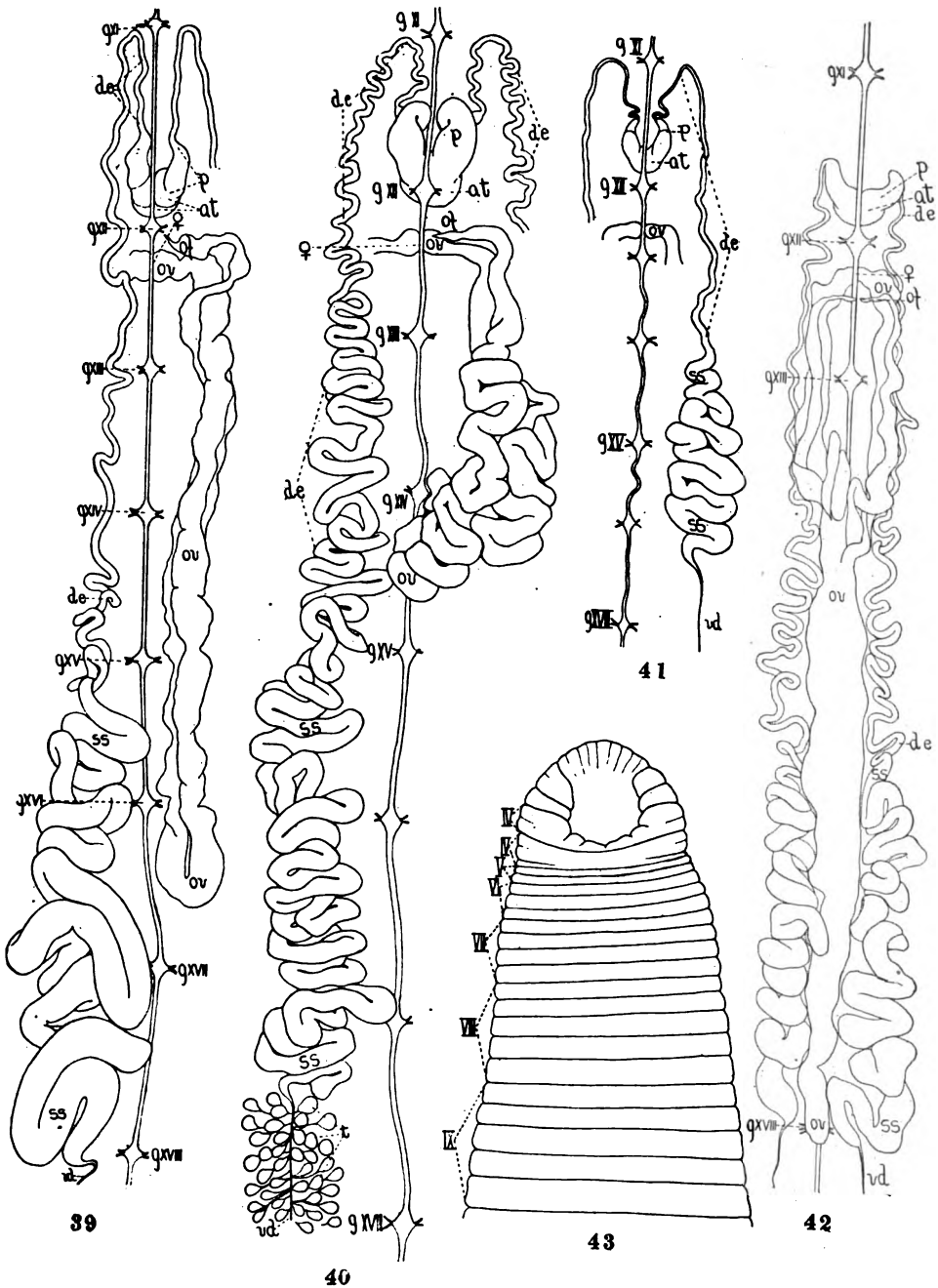
Fig. 41. Dorsal view of part of the reproductive organs.

### *Dina fervida.* x 7.5.

Fig. 42. Dorsal view of the reproductive organs. The testes and collecting portions of the vasa deferentia are not shown.

### *Dina parva.* x 22.5.

Fig. 43. The annulation of the anterior nine somites as seen from the ventral side.



*Erpobdella. Nephelopsis. Dina.*



















**Date Due**

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